RECRUITMENT MECHANISMS OF TANNER CRAB IN THE EASTERN BERING SEA

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A

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Abstract

Influences of biophysical conditions on survival of zoeal and early stages of eastern Bering Sea Tanner crab, *Chionoecetes bairdi,* were investigated using simple linear regression modeling, and a combination of hydrodynamic modeling and spatial and geostatistical methods. Linear regression analyses indicated that estimated reproductive female crab abundance, age 3-7 Pacific cod *(Gadus macrocephalus)* abundance and flathead sole *(Hippoglossoides elassodon)* total biomass were statistically related to estimates of recruitment to the 30-50 mm carapace width size interval of juvenile crab. Analysis of output from a Regional Ocean Modeling System simulation model indicated considerable capacity of the Bering Sea oceanography to retain zoeae at regional and local scales. Major transport patterns corresponded to long-term mean flows, with a northwesterly vector. Retention may be a significant recruitment process, particularly in Bristol Bay, which is effectively oceanographically isolated from other source regions of crab larvae. Periods during which conditions may have favored juvenile crab survival were observed at the model-estimated larval endpoints during the early 1980s and mid to late 1990s. While environmental conditions at model-estimated endpoints were highly variable, crab recruitment was positively correlated with endpoint locations either within the periphery of the cold pool, or outside of it, and SST >2° C after allowing for autocorrelation in the juvenile recruitment series. However, limitations of the model, gaps in knowledge of Tanner crab life history and ecology, and the possibility of spurious correlations complicate interpretation of these results.

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General Introduction

The eastern Bering Sea (EBS) Tanner crab stock has in recent decades experienced dramatic oscillations in recruitment, reflected by trends in the legal male segment supporting the fishery for this stock. This has created a "boom and bust" fishery, with multiple closures interspersed by years with good recruitment and economically valuable harvests (Stockhausen et al. 2013). Mechanisms responsible for this phenomenon are of both ecological and economic interest, as not only has the EBS Tanner crab fishery been of historic economic importance to local communities, but this recruitment variability has occurred within a backdrop of major, potentially related, ecosystem changes in the North Pacific and bordering seas (Hare & Mantua 2000, Mueter & Litzow 2008).

Recruitment to a given stock may be regulated by mechanisms that influence larval dispersal and retention trends, and by both pre- and post-settlement growth and mortality. For EBS Tanner crab, a modeling workshop (Tyler & Kruse 1997) has identified a number of likely recruitment mechanisms, which have been the basis of subsequent investigations (Rosenkranz et al. 1998, 2001, Zheng & Kruse 2006). Near bottom temperature and sea surface temperature are hypothesized to directly influence both growth and mortality through the thermal tolerances of the crabs themselves, but may also affect the predation and feeding environments (Smith & Vidal 1984, Rosenkranz 1998, Tyler & Kruse 1997, Ciannelli & Bailey 2005). Predation is likely to be an important source of mortality, and may comprise a recruitment mechanism. For instance, Pacific cod *(Gadus macrocephalus)* consumed 79% of a single cohort of juvenile Tanner crab in Marmot Bay, Alaska, over a 14-month period (Urban 2010). Based on stomach content analyses and modeling, cod and other groundfish are considered likely to be the most

important predators (Livingston 1989, Livingston et al. 1993, Lang et al. 2003, 2005), although cannibalism by older conspecifics may also be important (Jewett & Feder 1983, Sainte-Marie & Lafrance 2002). Fine grain sediments have been hypothesized to provide refugia for small crab, allowing them to bury themselves to avoid detection by predators (Rosenkranz 1998), though evidence for this is to date highly inferential, being based on observations of wind patterns that would drive Ekman Transport (Rosenkranz 1998; Rosenkranz et al. 1998, 2003) and observations of juveniles of the congener snow crab, *Chionoecetes opilio*, (Dionne et al. 2003). Finally, density-dependent stock-recruit relationships may arise through mechanisms besides cannibalism including disease (Siddeek et al. 2010) and competition for limiting resources including prey (Paul et al. 1979), although work to date has been inconclusive (Zheng & Kruse 1998, 2003).

A potential weakness in most pertinent research to date has been the use of adult recruitment as the measure of recruitment success, which increases the likelihood of confounding by secondary factors not included in the analysis (Rosenkranz 1998, Rosenkranz et al. 1998, 2001, Zheng & Kruse 2006). Information on approximate size-at-age and catchability-at-size may however allow the cautious development of a recruitment index based on younger crab, at least partially alleviating this concern (Donaldson et al. 1981, Somerton & Otto 1999, Rugolo & Turnock 2010).

Larval transport patterns are likely to be an important factor in determining crab recruitment patterns as they regulate post-settlement exposure to environmental recruitment factors that may vary in space and time. The interplay between retention and long-distance advection rates may comprise a recruitment mechanism, if, for instance, a long-term change in

drivers leads to a shift from local retention to sustained transport away from a given source area, while also isolating that area from importation of larvae from other sources (Cowen et al. 2003, Jones et al. 2005, Cowen et al. 2006, Lipcius et al. 2008, Cowen & Sponaugle 2009). If sustained large-scale transport occurs into an unfavorable habitat, such as the northern Bering Sea, or into the Bering Sea basin, regions not likely to favor a shelf-dwelling, subarctic species such as Tanner crab, transport has the potential to comprise a recruitment mechanism at the metapopulation level. Finally, a matter of some controversy is the degree to which the EBS Tanner crab metapopulation comprises one wholly intermixing population as opposed to a metapopulation comprised of at least two weakly connected subpopulations, which can have important implications for recruitment dynamics at both local and regional scales, and consequently, fishery management. Analysis of size frequency data has led some authors to conclude that there are in fact two substocks, broadly centered in Bristol Bay and near the Pribilof Islands (Somerton 1981). On this basis, the Alaska Department of Fish and Game manages the EBS Tanner crab stock as two substocks, one east and one west of 166°W longitude. Somerton (1981) did not, however, allow for migration with ontogeny, which may have introduced bias into that study. Genetic analyses have been inconclusive, with some supporting the division of the stock into substocks (Merkouris et al. 1998), and others not (Pritchard et al. 2000).

Advanced hydrodynamic modeling procedures provide a useful option for evaluation of larval transport and exchange within a greater metapopulation, and may be particularly applicable in the EBS region (Curchitser et al. 2005, Danielson et al. 2011). Here, the broad, low-gradient and relatively featureless continental shelf, in concert with low energy current

systems and limited potential for interactions with shorelines limit the formation of complex hydrodynamic features that might prove problematic to capture in the model environment. Hydrodynamic modeling also facilitates the direct investigation of spatial processes that may influence early life stage survival, through determination of environments that larvae and early juveniles are likely to have experienced (Parada et al. 2010). This contrasts with the more typical method of comparing aggregated recruitment data with aggregated environmental data, which assume spatial comparability among datasets and may leave unknown the actual overlap between conditions most likely to lead to mortality and the population of interest. Violation of this assumption has the potential to lead to erroneous conclusions pertaining to stock-environmental relationships.

In this dissertation I examined factors that have been hypothesized to comprise recruitment mechanisms through the application of several different methodologies, each constituting a separate chapter. Chapter one describes regression analyses conducted using generalized least squares (GLS) regression methods to compare a juvenile crab recruitment index reproductive female crab abundances and groundfish population size. Chapter two examines advection patterns and resultant trends in connectivity between subregions of the eastern Bering Sea and source-sink dynamics using output from a Regional Ocean Modeling System (ROMS) hydrodynamic model (Danielson et al. 2011). Chapter three explores relations between crab recruitment and a suite of environmental factors in a spatially explicit manner by utilizing output from the ROMS model to examine variability in biophysical conditions at the model estimated settling locations. In addition, appendices detail secondary analyses for each chapter that were not selected for inclusion in the chapters themselves.

Chapter 1:

Relationships Among Abundances of Juvenile Tanner Crabs, Spawning Adult Female Crabs, and Groundfish Predators in the Eastern Bering Sea[1]

Abstract

We investigated hypotheses concerning the effects of spawning female abundance and predatory groundfish abundance and biomass on juvenile recruitment of Tanner crabs, *Chionoecetes bairdi*, in the eastern Bering Sea (EBS). Hypotheses about causal relationships were tested using generalized non-linear least squares and generalized least squares procedures. Tanner crab abundance was estimated by area-swept methods using bottom trawl survey data, whereas stock assessment model estimates were employed for groundfish abundance and biomass. We found statistically significant negative relationships between juvenile crab recruitment and both spawning female crab abundance and flathead sole total biomass. We did not find robust evidence for statistically significant predatory effects by Pacific cod or yellowfin sole. Our findings suggest that predation by flathead sole may influence year-class strength of the EBS Tanner crab stock. While our results are consistent with the hypothesis of a negative stock-recruit relationship, interpretation is hampered by the possibility that recruitment is driven by long-term autocorrelated environmental factors that may generate the appearance of a density-dependent relationship when none exists.

[1] Richar, J.I., and Kruse, G.H. 2014. Relationships Among Abundances of Juvenile Tanner Crabs, Spawning Adult Female Crabs and Groundfish Predators in the Eastern Bering Sea. Prepared for submission to Marine Ecology Progress Series.

Introduction

The brachyuran Tanner crab, *Chionoecetes bairdi*, has supported a lucrative commercial fishery in the EBS since the 1960s. However, the EBS crab stock has experienced large-scale variability in recruitment and adult stock size. This has led to a "boom and bust" fishery, with contemporary peak landings of 30,209 t in 1977 and 18,189 t in 1990, followed by crashes leading to fishery closures in 1985-1986 and 1997-2004 (Rugolo & Turnock 2011). The stock declined below a minimum stock size threshold and was declared to be "overfished" in 2010. The fishery was subsequently closed during the 2010/2011, 2011/2012 and 2012/2013 fishing seasons. A reevaluation of the period used for estimating MSY-based reference points, coupled to a concurrent upgrade of the stock assessment from Tier 4 to Tier 3, led to a declaration that the stock was no longer overfished in October 2012, though the fishery remained closed during 2012-2013 season due to the Alaska Department of Fish and Game harvest strategy (Stockhausen et al. 2013). Such swings in stock status and management for the fishery underline the need to better understand stock productivity. Moreover, identification of potential causative mechanisms of variability in Tanner crab stock productivity is of significant interest due to the severe economic consequences of fishery closures on regional communities. In addition, the ecological relationships of crab population dynamics to other species and climate variability remain topics of speculation and ongoing research (e.g., Zheng & Kruse 2006).

Participants at a workshop on recruitment dynamics of Tanner crab suggested that the majority of mortality within an age class occurs during the early life stages, with the first year experiencing the highest mortality (Tyler & Kruse 1997). Mechanisms affecting

survival of age 0 to age 3 Tanner crabs are thus likely to exert the most significant effects on recruitment to the fishery, which has historically targeted mature males ≥ 138 mm carapace width (CW). Accordingly, early life history stages have been a focus of previous studies attempting to unravel the cause of fluctuations in crab abundance (Livingston 1989, Rosenkranz et al. 1998, 2001).

A 13-14 yr cycle is evident in both fishery recruitment and total adult population size and has been interpreted to indicate that long-term environmental variability may mediate recruitment strength (Zheng & Kruse 1998, 2003). This cycle is also approximately double the estimated mean age of maturity of female Tanner crabs in this region, suggesting the possibility of an endogenous rhythm associated in some way with a stock-recruit relationship. Previous studies have indicated a weak relationship between parental stock size and subsequent recruitment to the adult population at lags of 7-9 years, but large year-classes can result from both small and large breeding stocks (Zheng & Kruse 1998, 2003). Several issues hinder the ability to determine stock-recruit relationships. First, the relatively long time lags between reproduction and recruitment increase the potential for confounding by secondary mechanisms to blur processes operating during early life history. Second, the lack of age structures leads to uncertainty in the time from hatching to recruitment, necessitating inferences from modal analysis of size frequency distributions of a cohort observed repeatedly over time (e.g., Donaldson et al. 1981). Finally, owing to environmental and genetic variability in growth rates, members of multiple cohorts may recruit to the adult population within a given year (Rosenkranz 1998). The use of a smaller (younger) size class of crabs as an index of recruitment may be an important step in limiting the effects of such

concerns and determining potential recruitment controls. Using modeled juvenile recruitment to the age 4 yr post-settlement (age 5 yr post-fertilization) age class, Stockhausen (2013) found evidence for a Ricker-type relationship between juvenile crab recruitment and mature male crab biomass, while noting that the relationship between mature males and egg production, which they are assumed to index, is uncertain.

Predation by groundfish, in particular Pacific cod *(Gadus macrocephalus)*, flathead sole *(Hippoglossoides elassodon)*, and yellowfin sole *(Limanda aspera)* may be a significant source of mortality for juvenile Tanner crabs, as these species consume immature crabs in large quantities (Livingston 1989, Pacunski et al. 1998, Lang et al. 2003, 2005). Stomach contents suggest Pacific cod may remove up to 95% of age-1 (assumed to be 9-34 mm carapace width) crabs in some years, while also feeding on age 0 and 2 crabs at lesser rates (Livingston 1989, Urban 2010). However, retrospective correlative studies have failed to demonstrate a statistically significant negative relationship between groundfish biomass and recruitment of Tanner crabs; strong Tanner crab recruitment and high groundfish biomass have coincided in some years, which would not be expected if groundfish were significantly depleting young crabs through predation (Rosenkranz 1998, Kruse & Zheng 1999).

In this study we examined two null hypotheses concerning the effects of spawning female crab abundance and predation by three species of groundfish, Pacific cod, yellowfin sole and flathead sole, on the recruitment of juvenile Tanner crabs:

H_{01}: Recruitment strength of juvenile Tanner crabs is not strongly related to the size of the adult spawning population.

H_{02}: Recruitment of juvenile Tanner crabs is not related to population sizes of predatory Pacific cod, flathead sole and yellowfin sole.

Methods

Tanner Crab Abundance Estimates

Because a stock assessment model for EBS Tanner crab was under development at the time of this study (Rugolo & Turnock 2011), we estimated crab abundance directly by area-swept methods. Tanner crab data from an annual bottom trawl survey of the EBS continental shelf conducted by the National Marine Fisheries Service (NMFS) over 1978-2008 were provided by the NMFS Alaska Fisheries Science Center (AFSC). During the first decade of sampling the number of stations sampled varied, but has been standardized at 376 stations since 1988. A 0.5-hr tow is made near the center of each 20 x 20 nmi^2 (37 x 37 km^2) square on a sampling grid. Since 1982, the standardized sampling gear has been an eastern otter trawl using an 83 ft (25.m) head rope and a 112 ft (34.1 m) footrope (Rugolo & Turnock 2011).

We considered two primary classifications of Tanner crabs: juveniles and reproductively active females. For our purposes, we defined juvenile crab as those of both sexes with a CW of 30-50 mm. We did not utilize a smaller size interval because crabs smaller than this have very low catchability with trawl survey sampling gear. Modal analysis of instars observed off Kodiak Island in the Gulf of Alaska indicated that male crabs of modal sizes 31.6-53.6 mm CW were 21.1-37.3 months old (Donaldson et al. 1981), while a reduction in mean temperature from 6^o to 3^o C results in a near doubling of the intermolt period (Paul & Paul 2001). Consequently, we surmised that crabs within the 30-50 mm CW interval in the EBS are predominately 3 years of age post-hatching, based on extrapolation of the size-at-age

relationships derived for the Kodiak stock to cooler waters in the EBS. Due to uncertainty in this extrapolation, we also considered the possibility that 30-50 mm CW crabs were 2 or 4 years old, in our initial stock-recruit models.

Reproductively active female Tanner crabs were defined as those of shell condition 2 (SC2, new shell) bearing eyed eggs, shell condition 3 (SC3, old shell) and shell condition 4 (SC4, very old shell), summed by station. Shell-age classification approximates the time since the last molt using criteria described by Jadamec et al. (1999). Shell condition 2 female crabs bearing un-eyed eggs were ignored in our study as these are likely to be primiparous crabs. These have an extended brooding period, mating in late winter immediately following the terminal molt and carrying the resultant embryos until the following year (Swiney 2008). Consequently, primiparous females sampled in year *t* will hatch their eggs in year *t+1* and will not contribute to the hypothesized age 3 juvenile pseudocohort in year *t+3* used as the response variable in our stock-recruit analyses. Finally, SC5 crabs were ignored due to comparatively high rates of barrenness, lower fecundity and low abundance.

For each primary classification of crabs, mean density per station in year i ($\overline{D}_i$) was calculated as:

$$\overline{D}_i = \frac{\sum_j \sum_k \frac{S_{jk} * N_{jk}}{A_j}}{n_i}, \qquad \text{(eq. 1.1)}$$

where n_i= number of trawl stations sampled in year i where crabs were present, N_{jk} = number of crabs in size/SC class k sampled at station j, S_{jk} = the estimated sampling factor for crabs in size/SC class k at station j, used to account for subsampling based on sex, size and SC in the case of large hauls, and A_j = the estimated area swept at station j in km^2. For the juvenile

recruitment index, we modified eq. (1.1) to account for reduced catchability of the smaller juveniles (q = 0.30, Somerton & Otto 1999) compared to adult crabs:

$$\overline{D}_i = \frac{\sum_j \sum_k \frac{\frac{s_{jk} * N_{jk}}{q}}{A_j}}{n_i}, \qquad \text{(eq. 1.2)}$$

Annual area swept abundance estimates for a given year i (N_i) were then calculated as:

$$N_i = \sum_l \overline{D}_{il} * n_{il} * a, \qquad \text{(eq. 1.3)}$$

where N_i is the area swept abundance estimate for year i, $\overline{D}_{il}$ is the mean station density estimate in stratum l, n_{il} is the number of sampled standard grid squares within a given stratum l in year i and a is the area of the individual survey grid squares.

Due to the potential for regional differences in crab recruitment mechanisms, models were developed for three groups: “eastern”, representing the Bristol Bay subpopulation east of 166° W, “western”, representing the Pribilof Islands subpopulation west of 166° W longitude, and “EBS”, representing the entire EBS Tanner population (Fig. 1.1). This approach is consistent with current Alaska Department of Fish and Game (ADF&G) management policy for area-specific catch quotas. We excluded the 1982 female/1985 juvenile data point because the extremely large 1982 female abundance estimate (Fig. 1.3) is not consistent with size frequency distributions of crabs in the preceding years, which do not indicate a large maturing cohort in 1982 (Rugolo & Turnock 2011). Further, the >50% decline in the 1983 estimate relative to that of the preceding year far exceeds the currently accepted estimate of natural (females are not harvested) mortality (M = 0.23, Rugolo & Turnock 2011). Finally, due to the magnitude of the female estimate, inclusion of the 1982 female/1985 juvenile data pairing substantially inflated variance estimates, leading to a notably poorer model fit. Consequently

this data point was considered to be unreliable and was removed from primary S-R analyses for all three areas. However, we also conducted exploratory analyses including this data point and evaluated its consequences on model fit.

Groundfish Estimates

For groundfish, population estimates were taken from recent stock assessment model results for Pacific cod (Thompson et al. 2010), yellowfin sole (Wilderbuer et al. 2009), and flathead sole (Stockhausen et. al 2010). Due to the limitations of the data available, we used abundance anomalies for Pacific cod and yellowfin sole and biomass anomalies for flathead sole, for which abundance estimates were not available. We did not apply area-specific (i.e. eastern, western) population estimates for groundfish because estimates were reported only to the stock level, which spans the entire EBS shelf for all three species. Moreover, distributions and seasonal movements of all three species traverse the 166º W longitude line used to separate Tanner crabs in the eastern and western areas (Shimada & Kimura 1994, Nichol 1998, Stockhausen et al. 2010, Fig. 1.1).

For Pacific cod, we used abundance anomalies for ages 3-7 only, because cod of size 30-59 cm, generally corresponding to these ages, feed more heavily on juvenile Tanner crabs than those ≥ 60 cm (Livingston 1989). As mean age of 50% female maturity is 4.9 yr, our selected age range includes a mixture of immature and mature cod (Stark 2007). For yellowfin and flathead sole, we considered the minimum age capable of feeding on juvenile Tanner crabs based on mean fish length at age (Wilderbuer et al. 2009, Stockhausen et al. 2010), estimated maximum gape size based on visual comparison of mouth and body sizes, and mean crab size at age (Rugolo and Turnock 2010). Accordingly, we used abundance anomalies for age 7+

yellowfin sole and total biomass anomalies for age 3+ flathead sole to represent the age groups capable of consuming juvenile Tanner crabs.

Statistical Analysis Procedures

We employed generalized non-linear least squares (GNLS) and generalized least squares (GLS) procedures to examine relationships between juvenile crab recruitment and adult spawners, and between recruits (as prey) and several species of groundfish. To evaluate potential autocorrelation in recruitment, the sample autocorrelation function (ACF) was plotted for lags of 0 to 14 years. This revealed a significant positive autocorrelation at lag 1 yr, and a significant negative autocorrelation at lag 6 yr. Therefore, a first-order auto-regressive process was employed in all regression modeling, with the structure:

$$\varepsilon_t = \varphi\, \varepsilon_{t\text{-}1} + \nu_t\,, \qquad \text{(eq. 1.4)}$$

where ν_t is assumed to be a Gaussian white noise residual at time t with variance σ^2, and φ is the autocorrelation parameter ($|\varphi| < 1$) such that the residual variance is $\sigma^2\{\varepsilon_t\} = \frac{\sigma 2}{1-\varphi\, 2}$.

We explored multiple stock-recruit model formulations for applicability to our data. A linearized Ricker model was fitted to the Tanner crab data, with $\ln(R)$ as the response variable and abundance estimates for reproductive females as the explanatory variable (eq. 1.5).

$$ln(R) = \alpha + ln(S) - \beta S + \varepsilon_t, \qquad \text{(eq. 1.5)}$$

where R = juvenile crab recruits, S = reproductive female crab spawners, α = productivity at very low population sizes, β = parameter for density dependence and ε_t = the autocorrelated error term. Eq. (1.5) is the multiplicative Ricker model log-transformed for use in linear regression (Quinn & Deriso 1999, p. 104). Log-transformation of crab estimates within this

model formulation successfully resolved non-normality observed in initial exploratory analyses. Similarly, we fitted log-transformed Cushing models as (eq. 1.6):

$$ln(R) = \alpha + \beta * ln(S) + \varepsilon_t, \quad \text{(eq. 1.6)}$$

where parameters are as in eq. 1.5. In addition, we sought to fit a log-transformed Shepherd model (eq. 1.7).

$$ln(R) = \alpha - ln\left(1 + e^{g} * S^{\beta}\right) + \varepsilon_t, \quad \text{(eq. 1.7)}$$

where α, β, *R*, *S* and ε_t are as before, and g = a parameter controlling the shape of the stock recruit relationship; if $g > 1$, a domed Ricker relationship results, if $g = 1$ an asymptotic Beverton-Holt relationship results, and if $g < 1$, an unbound, concave, monotonic increasing relation results. Stock-recruit models were considered using lags of 2, 3 and 4 yr relative to spawner abundance and were fit using GNLS regression procedures , including specification of the AR(1) process as indicated in our autocorrelation analysis. To examine bias in stock-recruit model estimates, we compared stock-recruit residuals against juvenile abundance estimates.

Finally, in response to concerns about the possible effects of bias in S-R models, as an alternative to the S-R residuals we calculated a series of standardized anomalies in log-recruitment of juvenile crab for use in the predator-prey analyses (eq. 1.8).

$$r = \frac{ln(R) - \overline{ln(R)}}{s_{ln\,(R)}}, \quad \text{(eq. 1.8)}$$

where *R* is as before and $s_{ln\,(R)}$ is the standard error of the mean log-recruitment estimate.

For our predator-prey analyses we used generalized least squares (GLS) procedures incorporating the AR(1) autocorrelation process. Juvenile crab recruitment anomalies for each group (eastern, western, and total EBS) were regressed against each groundfish stock index at

lags corresponding to predation during the first and second years post-settlement. We explored two functional responses between predator and prey, the simplest being univariate models, representing simple linear relationships (eq. 1.9):

$$r = \beta_0 + \beta_1 X + \varepsilon_t, \quad \text{(eq. 1.9)}$$

where r = the juvenile log-recruitment anomaly, β_0 and β_1 are regression coefficients, X = the population estimate of the groundfish species and ε_t = the autocorrelated error term. We also explored polynomial regression models, employing both a linear and a quadratic term to allow for a domed relationship that may reflect prey-switching behavior of a generalist predator at high prey densities (eq. 1.10):

$$r = \beta_0 + \beta_1 X + \beta_2 X^2 + \varepsilon_t, \quad \text{(eq. 1.10)}$$

where β_2 is an additional coefficient, X^2 = the square of the population estimate to allow for curvature, and other terms are as in eq. (1.9).

Finally, statistical significance was evaluated at α = 0.05 for all S-R and predator-prey models using two-tailed *t*-tests. All analyses were completed using R version 2.14 (R Development Core Team 2005).

Results

Stock-recruit Relationships

Juvenile Tanner crab recruitment is characterized by large interannual variability with highest abundance in the late 1980s to early 1990s and in the early 2000s (Fig.1. 2). Recruitment patterns were similar in the eastern and western areas, but recruitment levels are generally higher in the western area especially after 1990. The abundance of reproductive

females has also experienced large variability, but with lower frequency (Fig. 1.3). Female abundance was relatively high in the early 1980s and early 1990s (Fig. 1.3).

Density dependence in the S-R relationship is suggested by a curvilinear relationship between the abundance of juvenile recruits and reproductive females in all three areas at lags of 2, 3 and 4 years (e.g., Fig.1. 4). Statistically significant Ricker stock-recruit relationships were observed in all three study groups at these lags (Fig.1. 5, Table 1.1), with both productivity and density-dependent terms being significant. Plots of residuals against observed juvenile estimates suggest model mis-specification due to the presence of significant bias in our model estimates, particularly at low spawner/high juvenile abundance levels (Fig.1.6), Further, decadal periodicity was observed in plots of stock-recruit model residuals for all three groups with peaks during the mid 1980s and late 1990s (Fig. 1.7). Significant autocorrelations were observed in both the EBS and western groups (Table 1.1). When we conducted the same S-R analyses with the outlier (1982 females, 1985 juveniles) included, poorer fits to both the western and EBS areas resulted, though the models remained significant and continued to display the cyclical patterns in the model residuals that were observed with the trimmed data series. The experimental fitting of a Cushing model to our data gave statistically significant results (Table 1.1). However the model was biologically nonsensical because it estimated a negative β parameter, which implies infinite recruitment at a spawning stock size of 0. The Shepherd model could not be fitted to our data due to non-convergence of the model fitting algorithm. Inherent in all stock-recruit models is the assumption that recruitment approaches zero as stock size decreases to very low levels; our data appear to violate this assumption.

Consequently, the juvenile log-recruitment anomaly series was selected for use in the groundfish predation analyses.

Groundfish Predator-Prey Relationships

Cyclical variability in the juvenile crab abundance residuals (Fig. 1.8a) did not clearly reflect trends in any single groundfish species (Fig. 1.8b, 1.8c, 1.8d). However, statistical relationships were observed between crab log-recruitment anomalies and abundance anomalies for Pacific cod as well as with total biomass anomalies of flathead sole (Table 1.2). Concerning the relationships of Pacific cod to the EBS group anomalies, a significant ($p = 0.02$) positive relationship was observed at lag-2 yr before recruitment for the linear term in both the simple linear and quadratic models, while the quadratic term was not significant ($p = 0.36$). At a lag of 1 yr, a statistically significant ($p = 0.04$) negative relationship was indicated for the quadratic term while the linear term was not significant ($p = 0.33$). Data points corresponding to cod abundance anomalies in 1978 and 1979 are major drivers of the negative relationships in these models (Figs 1.9, 1.10). After removing these data points from analysis, the quadratic term is no longer significant, while the positive linear relationship is strengthened ($p < 0.0001$).

For the eastern group, at lag-2 yr the linear term in both the linear and quadratic models was statistically significant ($p < 0.01$) and positive, while the quadratic term in the latter was not significant. In the corresponding lag-1 model, the linear term was not significant ($p = 0.93$), while the quadratic term was significant ($p = 0.04$) suggesting a dome-shaped relationship (negative coefficient) between crab log-recruitment anomalies and cod abundance. Similarly to the EBS group models, quadratic term significance in the eastern group was driven by data points for the 1978 and 1979 crab pseudocohorts. When these were removed, relationships

were no longer significant. Finally, for the western group, no Pacific cod models were significant (Table 1.2).

For flathead sole significant relationships were observed in both the western and EBS areas (Table 1.2). For the total EBS population, in both lag-1 and lag-2 models, quadratic terms were statistically significant ($p < 0.001$) and negative, implying a dome-shaped relationship between crab recruitment and flathead sole biomass, (Table 1.2). In the western area, quadratic terms were also statistically significant at both lags ($p = 0.004$, lag-1, $p = 0.01$, lag-2) and negative (Table 1.2). Finally, in the eastern area, only the lag-1 yr quadratic term was significant ($p = 0.05$) (Table 1.2). None of the simple linear regression models for flathead sole had a slope that was significantly different from zero (Table 1.2). Autocorrelation was a significant feature in all models, with variability in magnitude by region (Table 1.2). Consistent with these statistically significant relationships, a generally curvilinear relationship is apparent between flathead sole biomass and the crab anomalies for both areas, with a positive relationship at low sole biomass levels, and a pronounced negative trend at higher biomass levels (Fig. 1.11). Finally, no statistically significant relationships were indicated between yellowfin sole and log-recruitment anomalies for any of the Tanner crab groups (Fig. 1.12, Table 1.2).

Discussion

In this study, we examined possible stock-recruit and predator-prey relationships with recruitment and prey abundance defined as the estimated abundance of 30-50 mm CW juvenile Tanner crabs, representing approximately age-3 individuals. On this basis, our results are consistent with the presence of a strong negative density-dependent S-R relationship for the

Tanner crab population in the EBS, supporting rejection of $H_{01,}$ and a predatory effect by flathead sole, supporting rejection of H_{02}.

Density-dependent effects may result from several mechanisms. Synchronized release of larvae by dense aggregations of female crab may create dense patches of first-feeding zoeae that compete for prey (Stevens et al. 1994). Although there are no direct observations of this behavior in the EBS, as there are for Kodiak Island (Stevens et al. 1994), where a more constricted environment may lead to locally specialized behaviors, high density stations encountered during bottom trawl surveys are consistent with this behavior. It may thus be reasonable to expect that in the relatively sluggish currents over the EBS continental shelf, larvae could maintain dense aggregations. To successfully feed, larval Tanner crabs require high densities of copepods, potentially exceeding the mean concentration typically experienced in much of the natural environment (Paul et al. 1979, Incze & Paul 1983). In years of high reproductive output, zoeae in dense aggregations may thus experience increased mortality rates due to starvation as they draw down the local copepod population through feeding (Paul et al. 1979).

Alternatively, the negative relationship between recruitment and female abundance may arise from cannibalism (Jewett & Feder 1983, Sainte-Marie & Lafrance 2002, Nielson et al. 2007). In the conspecific snow crabs *(Chionoecetes opilio)*, both inter- and intra-cohort cannibalism have been observed, with inter-cohort cannibalism being the most significant (Sainte-Marie & Lafrance 2002). In laboratory treatments with nine or more instar V juveniles (~1 year old), instar I (newly settled) juveniles were completely extirpated, while the

prevalence of mutilation in survivors increased with density of the older year class (Sainte-Marie & Lafrance 2002).

In addition, changes in female spatial distributions associated with stock abundance may influence advection of larvae to suitable nursery areas. Generally, it is our observation that, in years when females are most abundant their distribution expands towards the outer shelf and northwest of the Pribilof Islands. Based on simulation results for snow crabs using a regional ocean modeling system, crab larvae released in these areas are more likely to be vagrants that are advected to the northern Bering Sea and off the shelf into the Aleutian Basin (Parada et al. 2010).

Alternatively, the conclusion of a density-dependent S-R relationship may be mistaken, despite the strength of the apparent relationships observed for Tanner crabs. In cases where recruitment variability is driven primarily by large-scale environmental factors that experience autocorrelated variability, an S-R relationship may be apparent, although none, in fact, exists (Walters 1990, Walters &Collie 1998). When the autocorrelation is associated with periodicity that approximates twice the mean generation time of the given species, an apparent relationship may be induced between spawners and recruits as spawner abundance cycles will tend to oscillate out of phase with the cycle of the given environmental factor (Shelton et al. 1985, Walters & Collie 1998). High spawner abundances resulting from successful year classes will appear associated with weak recruitment during periods when conditions are unfavorable, while resultant low spawner abundances will appear associated with strong recruitment in fact resulting from more favorable conditions (Walters & Collie 1998). The effect is to produce an

apparent S-R relationship resembling the descending limb of a Ricker curve where none, in fact, exists (Walters & Collie 1998).

The similarity between the example given in Walters & Collie (1998) and our data, and the periodicity of the residual cycle in our results which corresponds to approximately twice the female age of maturity, may indicate that our stock-recruitment relationship is in fact the result of an autocorrelated environmental factor, rather than an actual density-dependent relationship. In work not reported here, statistical relationships were found between stock-recruit residuals derived from a Ricker model and both the Pacific Decadal Oscillation and the Arctic Oscillation (Appendix A). The precise mechanism(s) by which these long-term climate patterns may affect Tanner crab however remain highly speculative, and follow up analyses employing the juvenile abundance anomaly series did not yield significant results.

Previous studies (Zheng & Kruse 1998, 2003) suggested only a weak S-R relationship for this Tanner crab population. However, the former analyses were based on results of a length-based stock assessment model for the eastern area (Bristol Bay) only; this model is no longer used because of subsequent spatial changes in the distribution of Tanner crabs currently exploited in the fishery. Our methods further differ in that we used estimated abundance of adult female crabs in "prime" reproductive condition (SC 3 and 4, plus SC 2 crabs carrying eyed eggs) and estimates of recruitment to the ~3-yr old age class. Zheng & Kruse (1998, 2003) estimated effective spawning biomass based on male and female abundance and assumed mating ratios and recruitment to the length-based model at lags of 7-9 yr, the latter of which likely increased the possibility of confounding from other mortality sources (Zheng & Kruse 1998, 2003).

We reject the null hypothesis of no predation effect in the case of flathead sole. Both the EBS and western groups demonstrated a dome-shaped relationship between the stock-recruit residuals and flathead sole biomass; models with lag-1 and -2 yr performed similarly. Crabs and soles may respond similarly to a common driver at low population levels, and then flathead sole may predate Tanner crab juveniles more heavily at high sole abundance levels. Interestingly, statistical significance was higher in the deeper waters found west of 166° W longitude, where flathead sole are more abundant and are prevalent year-round (Pacunski et al. 1998, Rooper et al. 2005). Among groundfish sampled annually for stomach analysis in the EBS, flathead sole are second only to Pacific cod in terms of Tanner crab predation, and they are occasionally the top predator of Tanner crabs (Lang et al. 2005).

Statistically significant relationships were found between Pacific cod and Tanner crab recruitment, and consequently, we reject H_{02} for Pacific cod. However, these relationships are not robust, becoming non-significant when one or two influential data points were removed. Moreover, positive relationships such as those we observed are inconsistent with the expected predator-prey response and may instead indicate the influence of a common control through bottom-up ecological processes (Worm & Myers 2003). Our results for cod largely agree with a previous retrospective analysis of Tanner crabs in the eastern (Bristol Bay) area, where no significant negative relationship between cod and crab recruitment was found (Rosenkranz 1998). In contrast, analysis of cod stomachs indicated intense predation by young cod on Tanner crabs, particularly for crab of age 1 yr (Livingston 1989). Those results were corroborated in subsequent stomach analyses with more recent data in the EBS Livingston et al. 1993, Lang et al. 2005) and Gulf of Alaska (Urban 2010).

Our results do not offer support for a significant predation effect on juvenile Tanner crabs by yellowfin sole, so we do not reject H_{02} for this species. This result is surprising considering both this species' prevalence within the study region (Wilderbuer et al. 2009) and stomach content analyses, which suggest this species consumes juvenile crabs (Livingston et al. 1993, Lang et al. 2005). Prevalence of crabs within yellowfin sole stomachs has however been highly variable interannually (Livingston et al. 1993, Lang et al. 2005), suggesting that predatory pressure may also be highly variable, possibly due to spatial dynamics that were not captured in our study. Yellowfin sole are seasonally migratory in response to the cold pool, with large numbers overwintering in deep offshore waters north of Unimak Island, and lower numbers in the outer domain west of the Pribilof Islands (Wilderbuer et al. 1992, Nichol 1998). These aggregations migrate inshore in the late spring and early summer, with the Unimak Pass group migrating towards Bristol Bay and the Pribilof Islands group following a more northerly route towards Nunivak Island (Wilderbuer et al. 1992). As these regions have not been important to regional trends in Tanner crab recruitment in recent years, it may be that heavy predation of Tanner crabs is limited to the migratory period when sole cross the shelf and is dependent upon prevalence of Tanner crabs within the migration corridors. Unlike flathead sole and Pacific cod, spatial distributions of yellowfin sole do not indicate large interannual variability, and do not appear responsive to variability in the extent of the cold pool (Spencer 2008).

Complexities present in predator-prey relationships may confound the ability to detect significant relationships in retrospective analyses such as ours. The degree of overlap between predator and prey may vary interannually, as both populations respond to dynamic

environmental conditions, and their respective environmental tolerances, with this reflected in predatory pressure experienced by the prey species (Ciannelli & Bailey 2005, Spencer 2008). If non-specialist predators experience a glut of prey items of various species, feeding pressure on a particular species might be reduced due to prey switching as predators optimize their foraging success (Krivan 1996). In addition, predator-prey relationships can be mediated through indirect effects by the presence of another predator (Siddon & Witman 2004), thus altering the observed functional response. Consequently, absence of an apparent predatory effect cannot be considered as conclusive evidence of a lack of a groundfish predation effect on recruitment strength of juvenile Tanner crabs.

Our research was complicated by several concerns. First, there was some uncertainty in determining age of the crabs as they do not retain hard body parts for age determination through molting. Second, due to variability in growth, it was not possible to accurately infer individual ages based on carapace width. We judged that a majority of crabs in the 30-50 mm CW size range would be age 3 based on size-at-age data for the Kodiak area in the northern Gulf of Alaska (Donaldson et al. 1981), coupled to recognition that colder temperatures were likely to be less favorable for growth in the EBS compared to the Gulf of Alaska, and the advice of crab experts (Dr. Robert Foy, NOAA, pers. comm., Dr. Jie Zheng, ADF&G, pers. comm.). Third, the survey sampling gear was size-selective for adult and subadult crabs; younger, smaller crabs were not fully represented in the catch (Somerton and Otto 1999). To compensate, we adjusted our juvenile index for the estimated catchability coefficient (q = 0.3), assuming constant catchability over time. The final juvenile crab index displayed trends somewhat similar to those experienced by the adult population 2-4 yr later,

and differences between the magnitudes of our estimates of juvenile and subsequent adult abundances were broadly consistent with current estimates of natural mortality (M = 0.23). Therefore, we feel that our estimates of juvenile abundance were reasonable. However, our recruitment estimates contrast strongly with those of Stockhausen (2013) and Stockhausen et al. (2013), who employed a statistical distribution to determine size-based entry into the stock-assessment model, in contrast to our "all-in" approach, which considered all crabs of size 30-50 mm CW to be recruits. Thus, the two recruitment indices are somewhat different entities. While the model of Stockhausen (2013) and Stockhausen et al. (2013) generally performed well, it had some difficulty replicating abundances of crab in the 30-50 mm CW interval, most notably during the mid to late 1980s (Stockhausen et al. 2013).

Our Ricker model recruitment estimates displayed notable bias, particularly at low spawner/high juvenile abundance levels, where juvenile abundance was consistently underestimated. We were limited in the selection of model structure by the apparent stock-recruit relationship, the need to meet the basic assumptions of a stock-recruit relationship (Haddon 2001, p. 249-250), and by technical difficulties preventing implementation of alternate model structures. Consequently due to the underlying stock-recruit model assumption of reduced recruitment at low stock sizes, it was not possible to implement a suitable model lacking bias.

In the work presented here, we did not consider effects of other environmental factors on Tanner crab recruitment. Previous studies found two statistically significant relationships with stronger Tanner crab recruitment: (1) warmer bottom temperatures, which may promote gonadogenesis and embryo incubation, and (2) northeasterly winds, which may favor offshore

advection to fine sediments or possibly coastal upwelling (Rosenkranz et al. 1998, 2001). A third relationship with warmer sea surface temperatures during the larval period, believed to favor production of copepod nauplii, was marginally non-significant after correction for autocorrelation in the time series. In an ongoing study, we are investigating these and other hypotheses with updated datasets. However, we anticipate that the greatest promise lies in recruitment investigations that consider the spatial scales at which the regulating processes operate. Detailed comparisons of spatial distributions of juvenile Tanner crabs, together with those of key limiting ecological factors, may be essential to more completely understand recruitment mechanisms that likely operate on finer-than-regional spatial scales and which likely vary interannually with changing oceanographic conditions. This approach may also resolve discrepancies in predation studies between stomach content analyses and statistical analyses, such as reported here.

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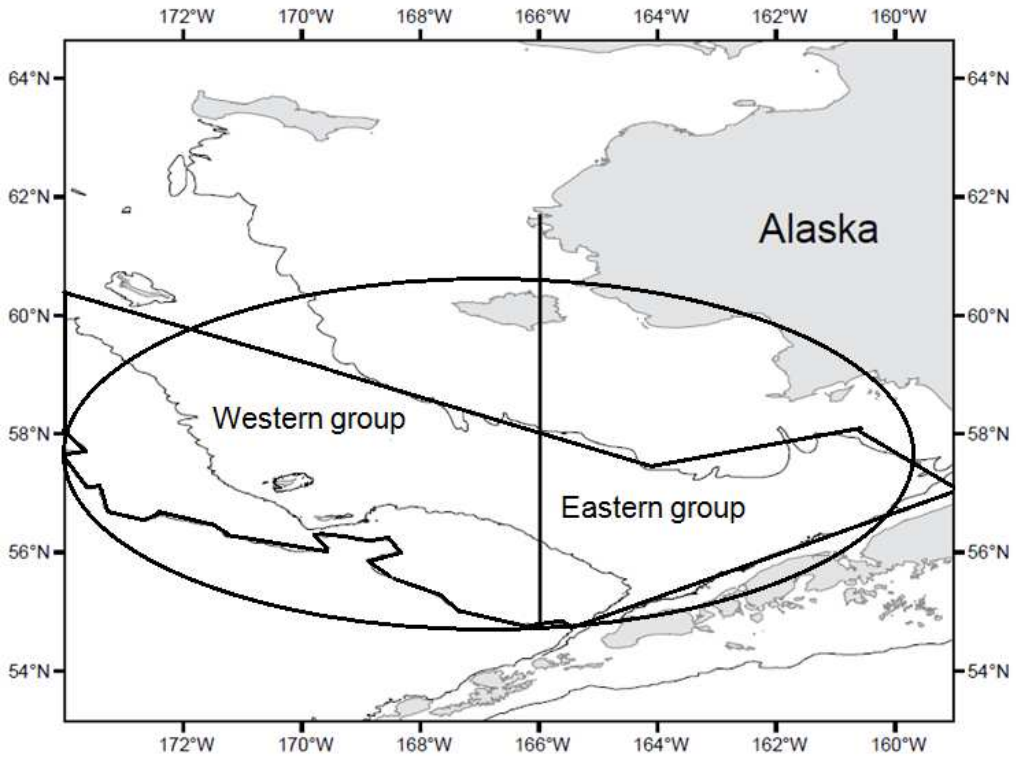

Figure 1.1. Study region and approximate distributions of subject species. Map of study region with 50-, 100- and 200 m isobaths, 166°W longitude (vertical line), approximate extent of eastern Bering Sea Tanner crab population (adults and juveniles, polygon), study sub-groups, and approximate range of groundfish predators (oval) . All three groundfish species are active within the on-shelf portions of this region on seasonal and interannual time scales.

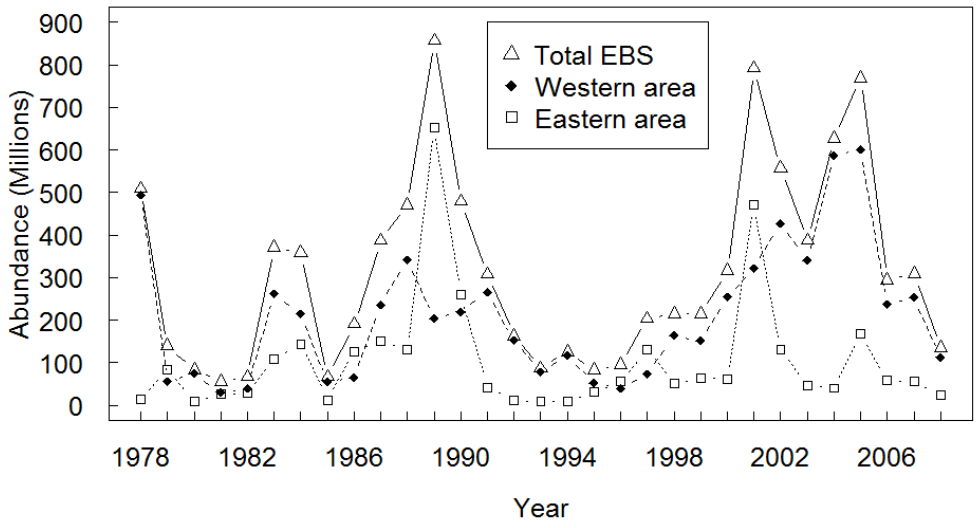

Figure 1.2. Regional abundance estimates of juvenile crab. Area-swept abundance estimates of 30-50 mm carapace width Tanner crab for the eastern, western, and total eastern Bering Sea (EBS) areas.

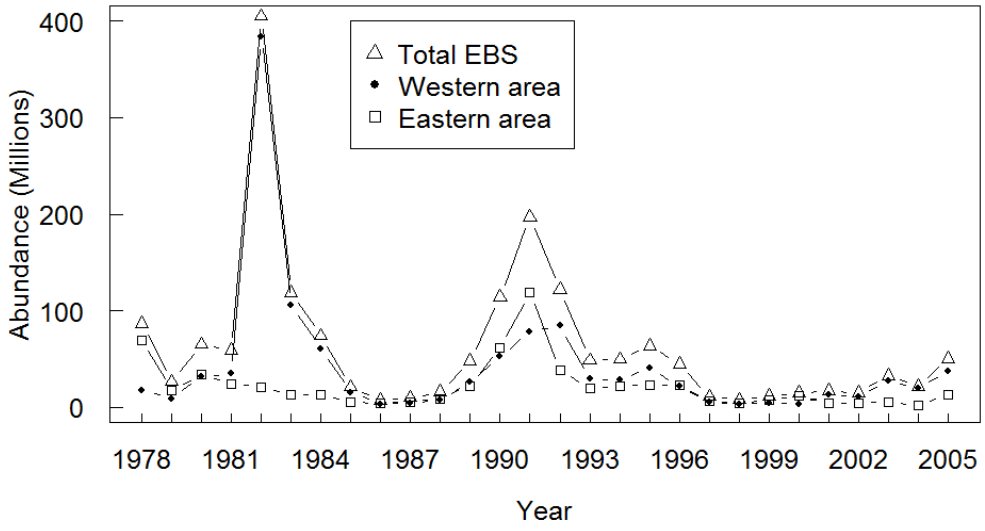

Figure 1.3. Regional abundance estimates of female crab. Area-swept abundance estimates of shell condition 3 plus shell condition 4 female Tanner crab for the eastern, western, and total eastern Bering Sea (EBS) areas.

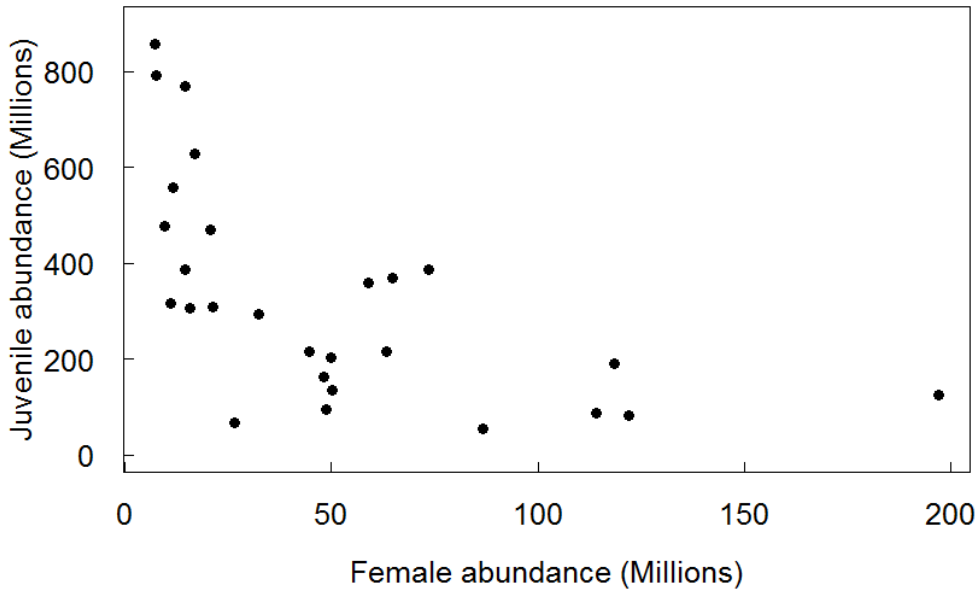

Figure 1.4. Comparison of juvenile abundance to female abundance. Juvenile Tanner crab abundance (lag-3 yr) versus abundance of reproductive female crab for the eastern Bering Sea (EBS) group. Relationships were similar for lags 2 and 4 yr and for the other groups.

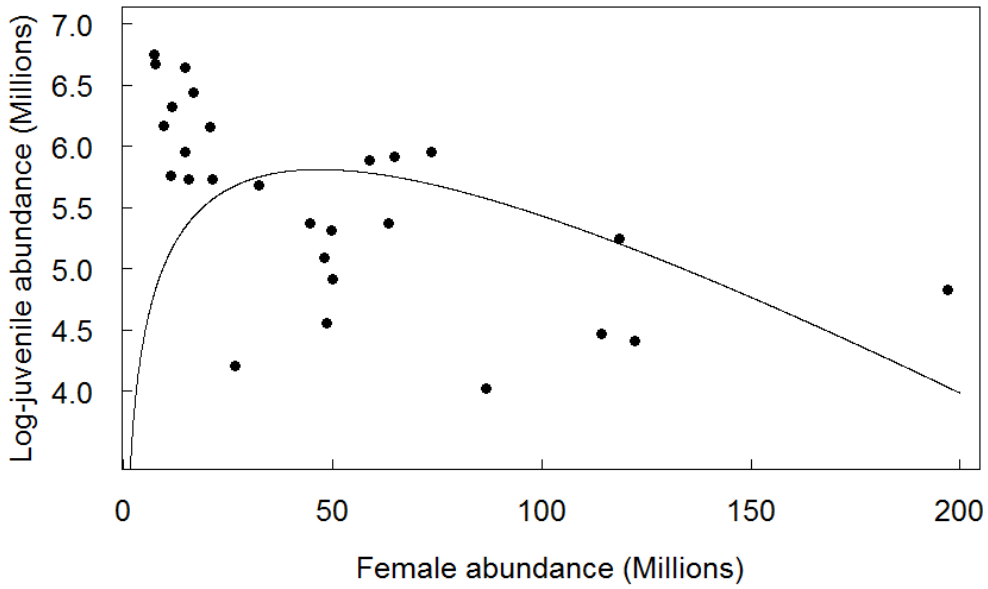

Figure 1.5. Comparison of juvenile crab log-abundance to female abundance. Natural logarithm of juvenile crab abundance versus abundance of reproductively active females at lag = 3 yr (shell condition 3 plus 4) for eastern Bering Sea (EBS) group with fitted Ricker model curve. Relationships were similar for lags 2 and 4 yr and for the other groups.

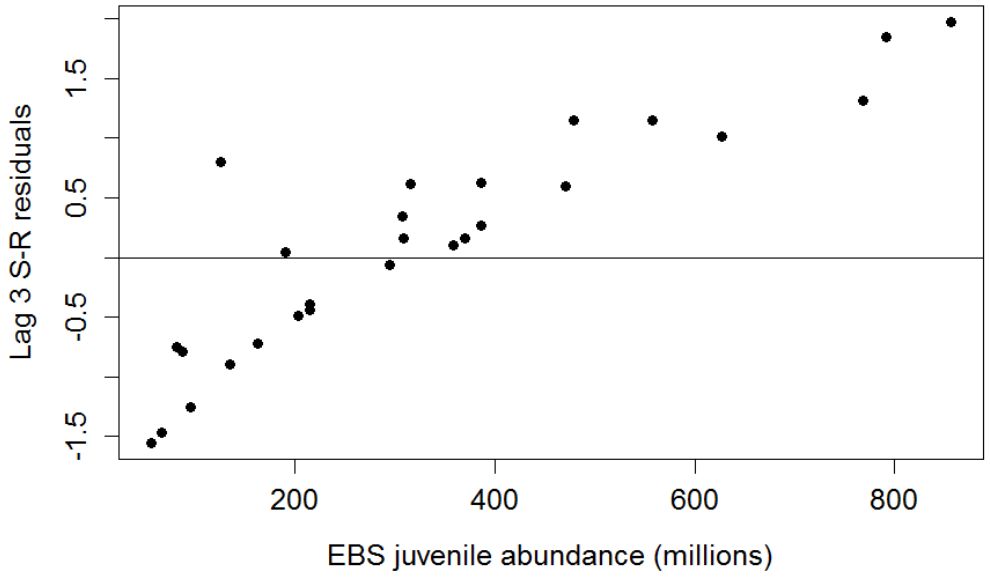

Figure 1.6. Comparison of model residuals against juvenile abundance. Lag 3 stock-recruit residuals from log-transformed Ricker model (eq. 1.5) for the EBS group versus abundance of juveniles. Horizontal line at $r = 0$ represents model trend line. Note consistent model underestimates at high juvenile abundance levels, in addition to a trend towards overestimation relative to population estimates at low abundances.

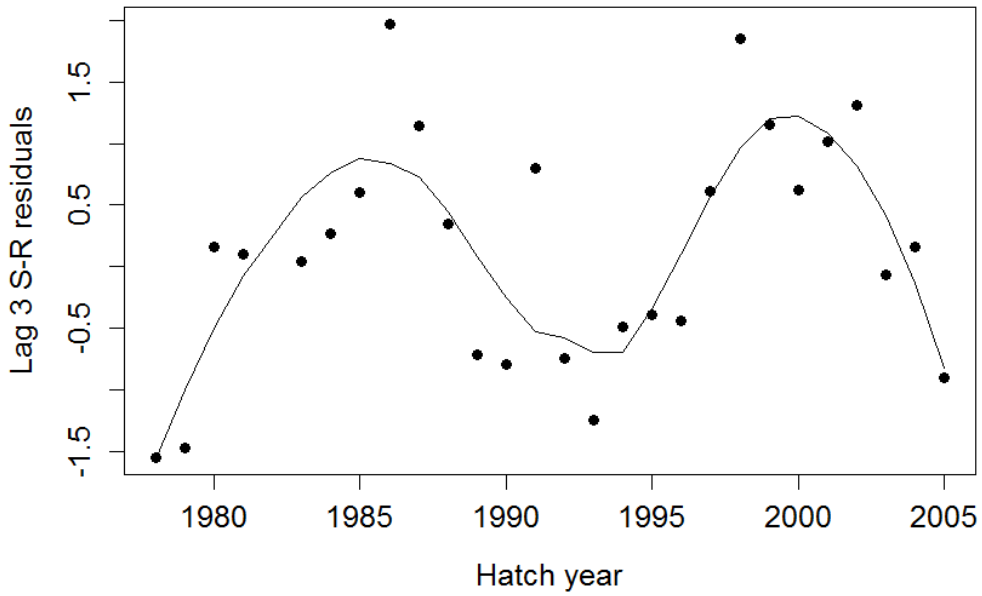

Figure 1.7. Stock-recruit model residuals. Trend in stock-recruit (S-R) residuals for the eastern Bering Sea (EBS) group, with LOWESS trendline.

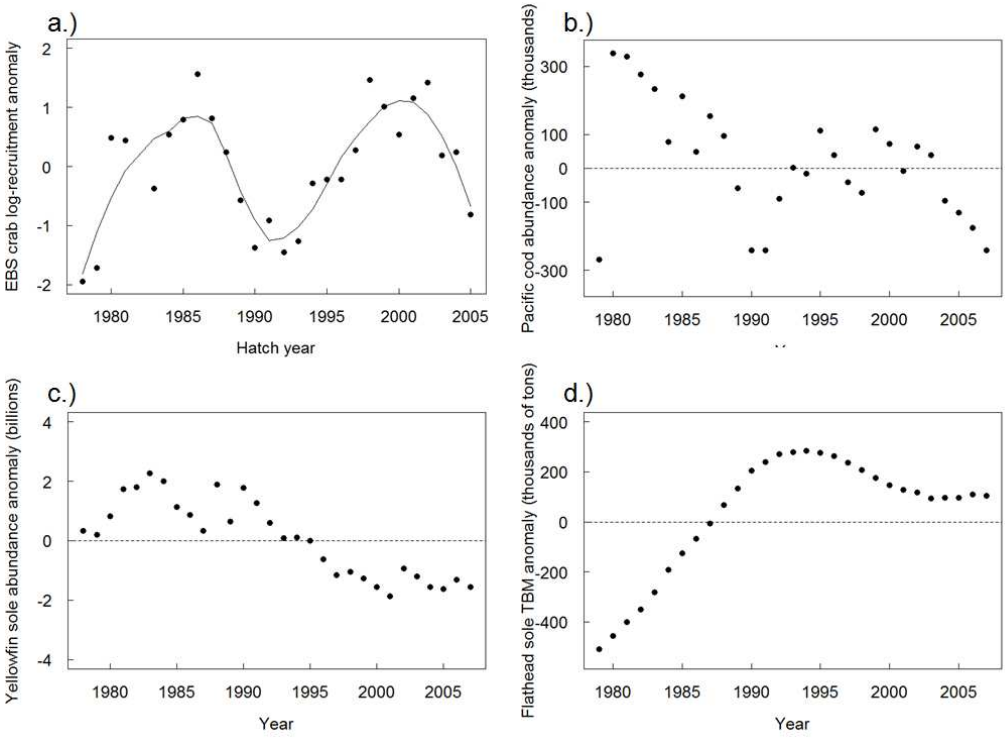

Figure 1.8. Subject species population trends. Trends in (a) juvenile log-recruitment anomalies for the eastern Bering Sea (EBS) group with LOWESS trendline, (b) abundance anomalies of eastern Bering Sea age 3-7 Pacific cod, (c) abundance anomalies of eastern Bering Sea age 7+ yellowfin sole, and (d) total biomass anomalies of eastern Bering Sea age 3+ flathead sole.

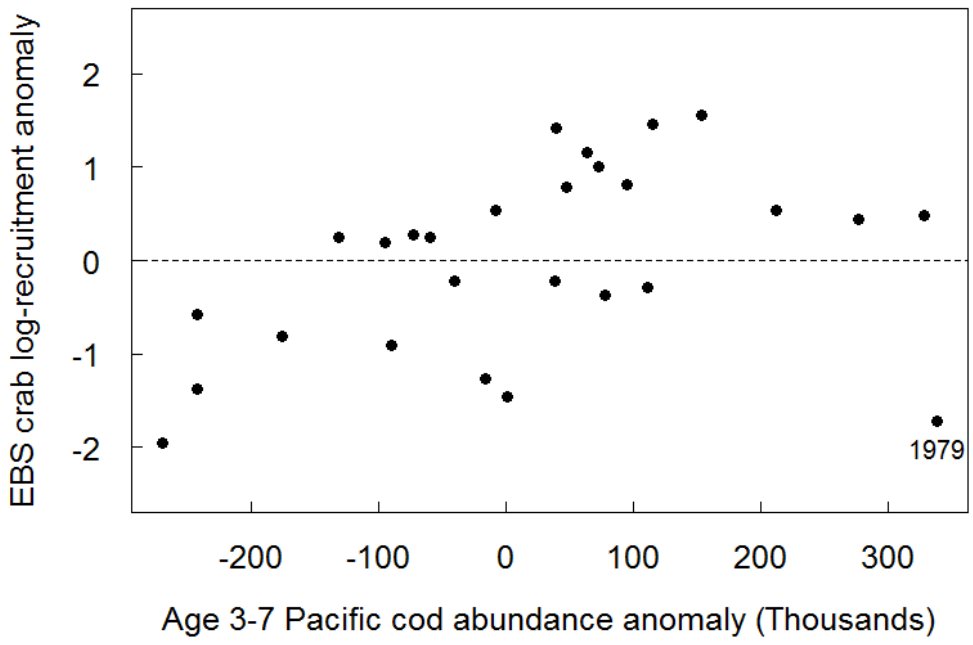

Figure 1.9. Eastern Bering Sea juvenile crab log-recruitment anomalies vs. Pacific cod abundance (lag-1 yr). Juvenile crab residuals for the eastern Bering Sea (EBS group) lagged to age 1 versus age 3-7 Pacific cod abundance anomaly.

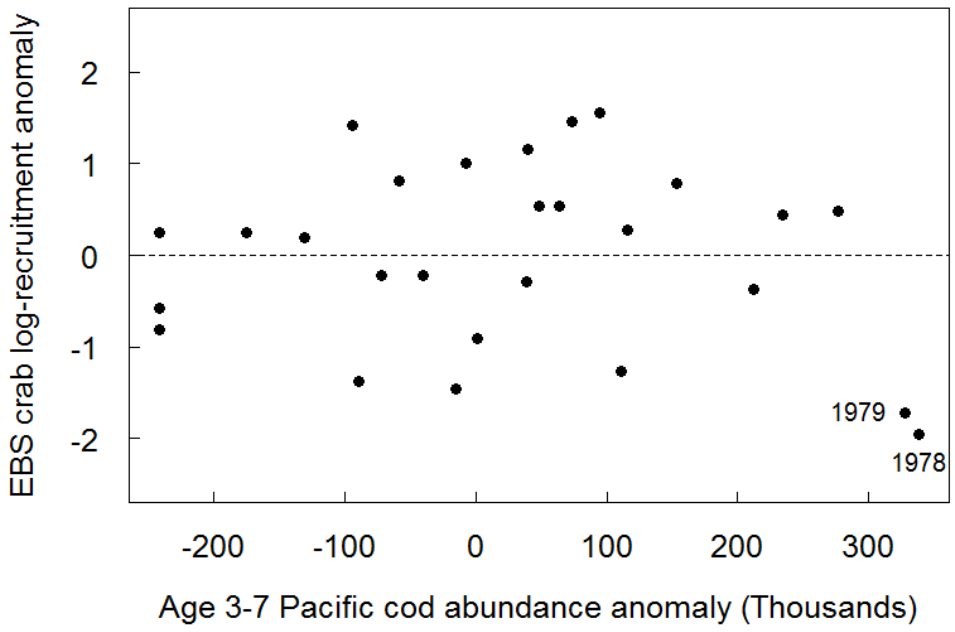

Figure 1.10. Eastern Bering Sea juvenile crab log-recruitment anomalies vs. Pacific cod abundance (lag-2 yr). Tanner crab stock-recruit (S-R) residuals for the eastern Bering Sea (EBS) group lagged to age 2 versus age 3-7 Pacific cod abundance anomaly.

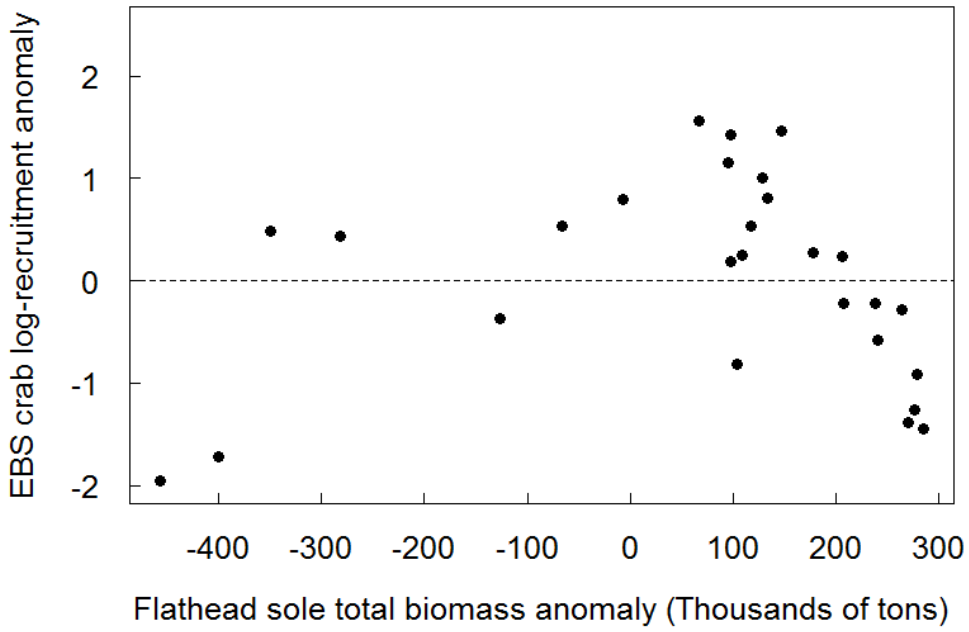

Figure 1.11. Eastern Bering Sea juvenile crab log-recruitment anomalies vs. flathead sole abundance. Tanner crab stock-recruit (S-R) residuals for the eastern Bering Sea (EBS) group lagged to age 2 versus total biomass of flathead sole.

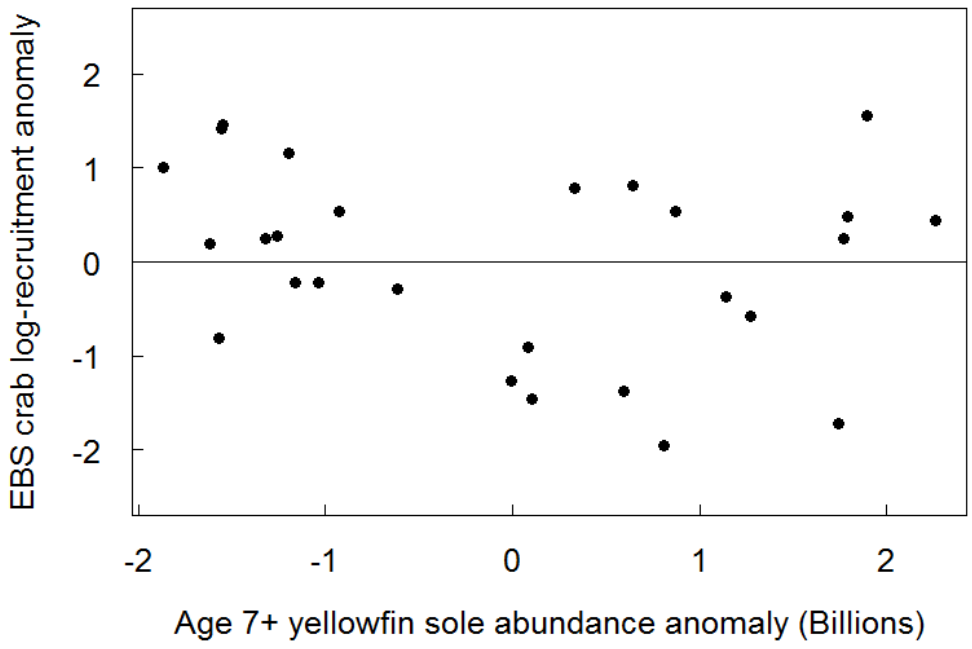

Figure 1.12. Eastern Bering Sea juvenile log-recruitment anomalies vs. yellowfin sole abundance. Tanner crab stock-recruit (S-R) residuals for the eastern Bering Sea (EBS group) lagged to age 2 versus age 7+ yellowfin sole abundance anomaly.

Table 1.1.Stock-recruit model parameter estimates and p-values. Model parameter estimates, parameter p-values (in parentheses) and autocorrelation terms, by lag (years) for Ricker and Cushing stock-recruit models for the eastern (east of 166^{o} W), western (west of 166 ^{o} W), and total eastern Bering Sea (EBS) areas.

Ricker									
Lag	Total EBS			Eastern Area			Western Area		
(yr)	α	β	Φ	α	β	φ	α	β	φ
2	3.01 (< 0.0001)	0.23 (<0.0001)	0.68	2.60 (< 0.0001)	5.27e-1 (<0.0001)	0.28	3.14 (<0.0001)	3.68e-1 (<0.0001)	0.66
3	2.97 (<0.0001)	2.14e-2 (0.0001)	0.58	2.60 (<0.0001)	4.70e-1 (<0.0001)	0.34	2.95 (<0.0001)	3.56e-1 (<0.0001)	0.77
4	3.23 (<0.0001)	2.45e-1 (<0.0001)	0.36	2.51 (<0.0001)	0.44 (0.0003)	0.26	3.02 (<0.0001)	2.99e-1 (0.002)	0.58
Cushing									
Lag	Total EBS			Eastern Area			Western Area		
(yr)	α	β	φ	α	β	φ	α	β	φ
2	3.77 (< 0.0001)	-5.02e-1 (0.003)	0.31	1.94 (< 0.0001)	-7.03e-1 (0.001)	0.05	2.86 (<0.0001)	-2.33e-1 (0.17)	0.57
3	3.82 (<0.0001)	-5.05e-1 (0.001)	0.41	2.00 (<0.0001)	-5.63-1 (<0.01)	0.43	2.81 (<0.0001)	-1.76e-1 (0.29)	0.58
4	3.80 (<0.0001)	-4.70e-1 (0.004)	0.32	1.91 (<0.0001)	-4.84e-1 (0.06)	0.39	2.99 (<0.0001)	-3.17e-1 (0.10)	0.32

Table 1.2. Predator-prey model parameter estimates and p-values. Model parameter estimates and p-values (in parentheses by time lags (years)) for linear and polynomial predator-prey models for Tanner crab (prey) in the eastern (east of 166° W), western (west of 166° W), and total eastern Bering Sea (EBS) areas involving predators (x_i): (a) Pacific cod, (b) yellowfin sole, and (c) flathead sole.

Model	Eastern Area			Western Area			Total EBS		
	β_1	β_2	φ	β_1	β_2	φ	β_1	β_2	φ
				a. Pacific cod					
Lag 2	2.96e-6		0.51	1.53e-6		0.73	2.24e-6		0.76
	(0.006)			(0.15)			(0.02)		
Lag 2	2.54	-1.53	0.39	1.25	-5.66e-1	0.69	1.85	-9.92e-1	0.69
Polynomial	(0.003)	(0.09)		(0.16)	(0.60)		(0.02)	(0.36)	
Lag 1	8.40e-7		0.63	-1.90e-6		0.72	5.30e-7		0.79
	(0.59)			(0.22)			(0.73)		
Lag 1	1.17e-1	-2.33	0.65	-2.07	-1.69	0.77	-1.20	-2.23	0.73
Polynomial	(0.93)	(0.04)		(0.10)	(0.13)		(0.33)	(0.04)	
				b. Yellowfin sole					
Lag 2	-2.83e-2		0.66	2.08e-2		0.75	-7.94e-5		0.80
	(0.90)			(0.93)			(0.99)		
Lag 2	-3.05e-1	1.73e-1	0.66	1.13e-1	-1.72e-1	0.77	3.73e-1	-3.12e-1	0.83
Polynomial	(0.86)	(0.85)		(0.95)	(0.84)		(0.84)	(0.71)	
Lag 1	8.08e-2		0.67	-1.13e-1		0.73	-1.02e-1		0.83
	(0.73)			(0.68)			(0.66)		
Lag 1	-2.06e-1	1.06	0.65	-1.89	1.35	0.77	-7.98e-1	1.34	0.76
Polynomial	(0.90)	(0.23)		(0.23)	(0.10)		(0.63)	(0.09)	
				c. Flathead sole					
Lag 2	-4.80e-7		0.70	7.50e-7		0.77	1.00e-7		0.86
	(0.78)			(0.70)			(0.95)		
Lag 2	-1.48	-3.04	0.68	6.69e-1	-3.12	0.49	8.12e-2	-3.53	0.58
Polynomial	(0.45)	(0.06)		(0.60)	(0.01)		(1.00)	(0.006)	
Lag 1	-1.90e-7		0.69	7.10e-7		0.77	5.00-7		0.84
	(0.91)			(0.73)			(0.83)		
Lag 1	-9.84e-1	-2.87	0.58	6.65e-1	-3.25	0.80	2.95e-1	-3.66	0.44
Polynomial	(0.53)	(0.05)		(0.55)	(0.004)		(0.78)	(0.0009)	

Chapter 2:

Patterns in Connectivity and Retention of Simulated Tanner crab *(Chionoecetes bairdi)* Larvae in the Eastern Bering Sea[1]

Abstract

The eastern Bering Sea (EBS) population of Tanner crab (*Chionoecetes bairdi*) exhibited high variability in recruitment to the commercially exploited stock since the late 1970s. Cyclical variability in large male crab abundance led to a boom-and-bust fishery, the causes of which remain poorly understood. The Regional Ocean Modeling System (ROMS) was used to simulate larval Tanner crab advection patterns over 1978 □ 2004 based on larval hatching sites inferred from the distributions of reproductive females sampled during annual National Marine Fisheries Service trawl surveys. Connectivity among EBS subregions was examined by comparing start and end float locations after 60 days of simulated drift at four depth intervals corresponding to depths at which floats were held: bulk (all depths combined), 10 m, 30 m and 50 m. High levels of retention (>50% of floats) were observed in the majority of source subregions. Patterns in advection and resultant interregional connectivity were highly variable. Modeled retention within the overall EBS study region was lowest in the early 1980s, but never < 70%. The Pribilof Islands area became much more important than Bristol Bay for settlement after 1990, consistent with an observed geographic shift in recruitment strength. Apparent reliance of Bristol Bay on local larval retention validates recent spatial fishery management to conserve this area as a subpopulation.

[1] Richar, J. I., Kruse, G.H., Curchitser, E., and Hermann, A.J. 2014. Patterns in Connectivity and Retention of Simulated Tanner crab (*Chionoecetes bairdi*) Larvae in the Eastern Bering Sea. Submitted to Progress in Oceanography.

Introduction

Knowledge of connectivity, the exchange of individuals within a metapopulation, is a key step toward understanding recruitment dynamics in marine species. Many marine organisms produce meroplanktic larvae, which may remain in the water column for time periods ranging from several days to several months and may be advected across distances ranging from a few to hundreds of km (Becker *et al.*, 2007; Siegel *et al.*, 2003; Sponaugle *et al.*, 2002). Oceanographic processes and larval behavior often foster more localized larval retention than expected based on considerations of mean current velocity and direction during the larval period, leading to the structuring of metapopulations into smaller primarily self-recruiting subpopulations (Becker *et al.*, 2007; Blanton *et al.*, 1995; Cowen *et al.*, 2003, 2006; Crawford and Jamieson, 1996).

The interplay between retention and long-distance advection rates may be a significant driver of recruitment dynamics, particularly at the reduced spatial scales characteristic of local populations (Cowen *et al.*, 2006; Cowen and Sponaugle, 2009; Jones *et al.*, 2005; Lipcius *et al.*, 2008). Local populations may also be sustained by ontogenetic migrations, whereby maturing individuals migrate "upstream" from nursery habitats to spawning habitats where their life cycle begins once again (Hinckley *et al.*, 2001, Parada *et al.*, 2010; Sponaugle *et al.*, 2002). Finally, these populations may be sustained through delivery of larvae from one or more external source regions (Cowen *et al.*, 2006; Jones *et al.*, 2009; Stockhausen and Hermann, 2007). These delivery mechanisms are themselves influenced by processes that may vary in space and time, making it challenging to discern their roles in determining recruitment success. Understanding the relative importance of each of these mechanisms in determining the degree

of connectivity in a given population is an important step toward understanding the dynamics of that population.

In recent years, the eastern Bering Sea (EBS) population of Tanner crab, *Chionoecetes bairdi*, has exhibited great variability in survival to maturity and subsequent recruitment to the legal adult male population component that forms the basis of the historically valuable fishery (Rugolo and Turnock, 2011). Recruitment variability is associated with a "boom and bust" fishery, with historical peak landings of 30,209 t in 1977 and 18,189 t in 1990, followed by stock declines and fishery closures in 1985-1986, 1997-2004 and 2011-present (Rugolo and Turnock, 2011; Stockhausen *et al.*, 2013). A disproportionate decline in abundance in Bristol Bay, coupled to a southwesterly, offshore shift in abundance to deeper waters, was associated with recent stock declines (Zheng, 2008).

As with other species, spatial distributions of both immature and mature Tanner crabs vary interannually, possibly due to a combination of year-to-year variability in the location of hatching sites, advection patterns during the 2-mo larval stage, and differential spatiotemporal patterns in post-settlement survival. This raises the question of "downstream effects" – namely, does variability in spatial patterns of settling megalopae influence subsequent advection of the next generation of progeny as they mature and become reproductively active, leading to variable patterns in connectivity over time? Specific to EBS Tanner crab, might variable patterns in connectivity explain the observed collapse of the subpopulation within Bristol Bay coincident with the offshore shift in the adult crab population since 1990? Knowledge of connectivity between, and retention within, subunits of the EBS Tanner crab metapopulation may help answer these questions and provide insight into spatial management considerations.

Eastern Bering Sea Tanner crab larvae hatch during mid to late spring (Incze *et al.*, 1987). Larval crabs develop through two zoeal stages, each of approximately 1 mo duration, before molting into a megalops stage of unknown duration (Incze *et al.*, 1982), during which larvae may remain planktic or settle out of the water column, presumably based on environmental cues signaling benthic habitat suitability, as in the congener *Chionoecetes opilio* (Dionne *et al.*, 2003; Incze *et al.*, 1982). Upon becoming benthic, Tanner crabs molt through a series of up to 17 instars before attaining terminal molt (Rugolo and Turnock, 2011). Females are believed to mature at an age of approximately 6 yr, whereas males are thought to mature at approximately 7-8 yr, at which point mating may occur (Donaldson *et al.*, 1981; Rosenkranz *et al.*, 1998).

The EBS continental shelf is subdivided into three distinct domains based on water column structure and chemistry: the inner, middle, and outer domains, each with a characteristic current regime (Coachman, 1986). Two fronts, located at approximately the 50- and 100-m depth contours, separate these three domains and may act to impede exchange of larvae among domains (Coachman, 1986; Galarza *et al.*, 2009; Sebates and Olivar, 1996; Sponaugle *et al.*, 2002). The outer domain is further delineated from the Bering Sea basin by a shelf-break front occurring at ~170 m, acting as an additional boundary between the continental shelf and off-shelf waters (Stabeno *et al.*, 1999).

Tidal currents predominate in the inner domain, accounting for ~95% of the flow energy within this region (Coachman, 1986). However, a weak (1-5 cm/s) mean flow exists, following the 50-m isobath northward (Fig. 2.1). In the middle domain, tidal currents dominate, while net flow is minimal because weak (~2-3 cm/s) and variable wind-driven flows tend to

cancel out (Coachman, 1986). A combination of sluggish advection rates and low bottom relief results in a relatively long residence time (~1 yr) for water within this region, allowing for the persistence of winter conditions known as the "cold pool" in the bottom layer (Schumacher *et al.*, 1979). Tidal currents account for ~80% of flow in the outer domain, with a ~5 cm/s mean northwesterly flow along the shelf (Coachman, 1986; Fig. 2.1). Water from the Bering Slope Current is believed to intrude onto the shelf at the Bering Canyon near Unimak Pass and west of the Pribilof Islands, where a narrowing of the shelf break accelerates current flow along the 100 m isobath, which subsequently turns northward, thus directing flow onto the shelf near St. Matthew Island (Stabeno *et al.*, 1999; Fig. 2.1).

Recent advances in computer technology and a better understanding of ocean dynamics have facilitated the development of increasingly realistic simulation models. Consequently, 3-D oceanographic models have been increasingly used to explore advection of marine fish and invertebrate larvae worldwide, providing valuable insights into recruitment dynamics (Cowen *et al.*, 2007; Cowen and Sponaugle, 2009; Incze and Naimie, 2000; Pederson *et al.*, 2006). Several recent studies have been conducted employing variants of the Northeast Pacific (NEP) version of the Regional Ocean Modeling System (ROMS) (Curchitser *et al.*, 2005; Danielson *et al.*, 2011; Hermann *et al*., 2009), a Lagrangian hydrodynamic model, to investigate larval dispersal patterns through advection modeling (Cooper *et al.*, 2012; Parada *et al.*, 2010; Stockhausen and Hermann, 2007). Simulation models are also finding extensive application in examinations of population connectivity as an additional means of exploring source-sink larval dynamics as a complement to genetic and microchemistry approaches (e.g., Cowen *et al.*, 2007).

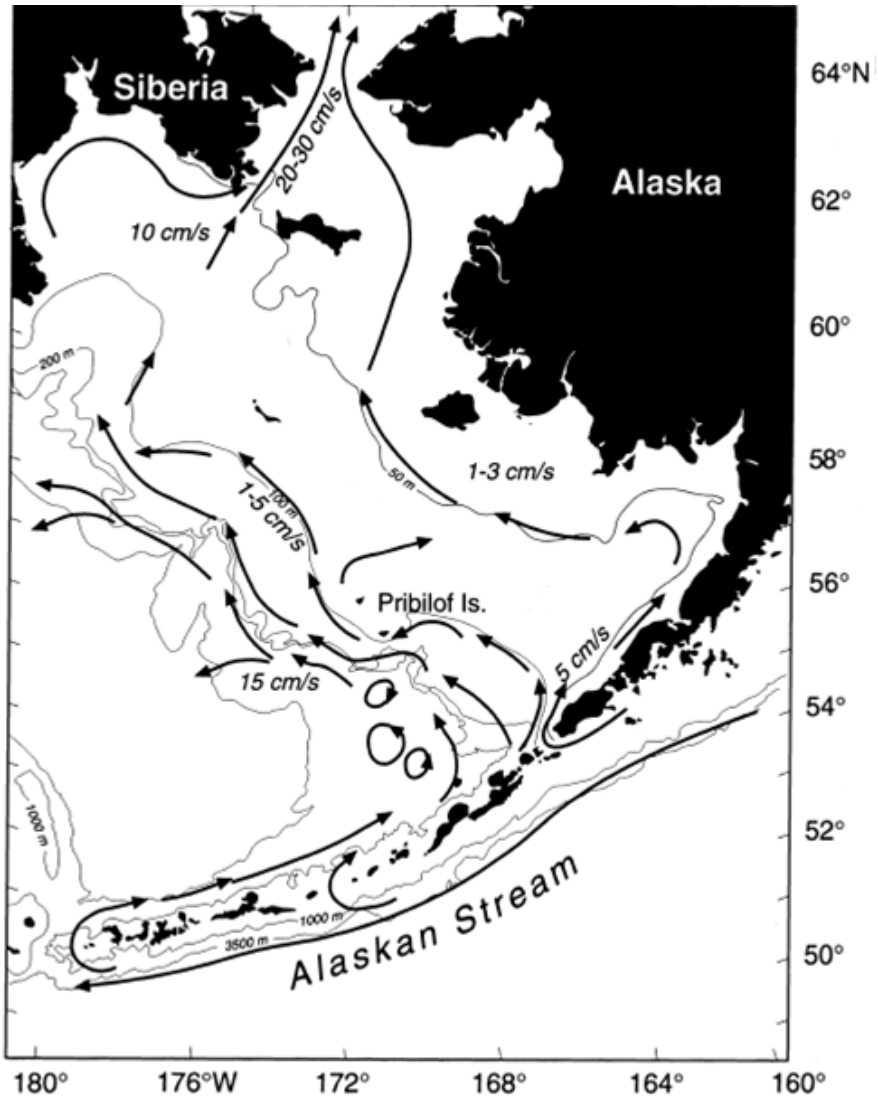

Figure 2.1. Eastern Bering Sea circulation patterns. Mean sustained circulation patterns in the eastern Bering Sea. Solid arrows denote currents with mean velocities > 1 cm/s (modified from Stabeno *et al.*, 2001).

The objectives in our study were twofold: (1) determine whether EBS Tanner crabs comprise a single metapopulation well connected by larval advection; and (2) examine the relative importance of connectivity and retention within the management subregions east and west of 166° W longitude.

Methods

Tanner Crab Density and Abundance Estimates

We estimated EBS Tanner crab abundance directly by area-swept methods using data from the National Marine Fisheries Service (NMFS) summer bottom trawl survey over 1978-2004. There was variability in the number of stations sampled prior to 1988; since then, the number of stations has been standardized at 376. A 0.5-hr tow was made near the center of each 20 x 20 nmi^2 (37 x 37 km^2) square on a sampling grid. Since 1982, the standardized sampling gear has been an eastern otter trawl with an 83 ft (25 m) head rope and a 112 ft (34.1 m) footrope (Rugolo and Turnock, 2011).

For our purposes, reproductively active female Tanner crabs were taken to be those of primarily shell condition 3 (SC3, old shell) and 4 (SC4, very old shell) (see Jadamec *et al.*, 1999 for descriptions of shell conditions). Shell condition 2 females carrying eyed embryos were also included; this is an indication that these females mated the previous season (*t*-1) and will thus hatch their clutch in year *t*. Shell condition 2 females carrying uneyed embryos were ignored as they likely represent primiparous females that have an extended brooding period; such crabs, sampled in year *t* will hatch their eggs in year *t+1* as SC3 females, rather than in year *t*, and would thus not contribute to reproductive output in year *t*. Shell condition 5 females were ignored due to both low abundances and high rates of barrenness. SC4 female abundance

was weighted relative to SC3 abundance to adjust for reduced fecundity and egg bearing rates (Joel Webb, Alaska Department of Fish and Game, pers. comm.) using eq. (1):

$$SC4_w = \left(\frac{SC4_f}{SC3_f}\right) * \left(\frac{SC4_{eb}}{SC3_{eb}}\right), \quad \text{[eq. 2.1]}$$

where $SC4_w$ is the weight function by which SC4 female density estimates were multiplied to standardize their reproductive potential relative to SC3 females, $SC3_f$ = shell condition 3 female fecundity, $SC4_f$ = shell condition 4 female fecundity, $SC3_{eb}$ = shell condition 3 egg bearing rate and $SC4_{eb}$ = shell condition 4 egg bearing rate. Abundances of SC3 and weighted SC4 abundances were then summed together to obtain overall station abundance from which we estimated density at station *i* in year *j* ($\widehat{D}_{ij}$, eq. 2):

$$\widehat{D}_{ij} = \frac{\sum_k S_{ijk} * N_{ijk}}{A_{ij}}, \quad \text{[eq. 2.2]}$$

where N_{ijk} = number of crabs in class *k* sampled at station *j* in year *i*, S_{ijk} = the estimated sampling factor for crabs in class *k* at station *j* in year *i*, and A_{ij} = the estimated area swept at station *j* in year *i*, in km^2. The sampling factor expands the number of crabs sampled for biological information and listed in the database to the number actually captured by the trawl tow at that station in cases of large hauls.

Regional Ocean Modeling System

We employed a variant of ROMS known as the Northeast Pacific Model-5 (NEP5), which was developed as a part of the Northeast Pacific Global Ocean Ecosystem Dynamics (GLOBEC) and Bering Ecosystem Study (BEST) research programs (Curchitser *et al.*, 2005, Danielson *et al.*, 2011). The NEP5 is a free-surface hydrostatic primitive equation ocean circulation model with a 10-km grid used to simulate current patterns based on environmental

forcing variables. Model equations are horizontally discretized across a staggered Arakawa C-grid using boundary fitted orthogonal curvilinear coordinates (Danielson *et al.*, 2011). Vertically, the model equations are discretized over bathymetric features by means of a terrain-following coordinate system able to increase model resolution near comparatively complex layers at the surface and bottom of the water column. Our implementation employed 10 vertical layers to capture variability in water column features. Surface forcing for NEP5 is implemented using data obtained from the Common Ocean-ice Reference Experiments (CORE, Large and Yeager, 2008) including observations of wind direction and magnitude at 6-hr intervals, atmospheric temperatures, sea level pressure, specific humidity, daily short-wave and downwelling long-wave radiation and monthly precipitation levels (Danielson *et al.*, 2011). River discharge is implemented within the model as a spatially dependent, constant surface freshwater flux that preserves fresh water budgets at the regional level, albeit at the expense of introducing inaccuracies into local salinity calculations (Danielson *et al.*, 2011). Tracer advection employs weakly dissipative algorithms which maintain sharp gradients across key oceanographic features, including the fronts separating the EBS domains (Danielson *et al.*, 2011).

Key model parameters for Tanner crab larvae, including float release timing, pattern of release, float depth distributions and advection duration, were derived separately from field observations (Incze *et al.*, 1987). Observations within the EBS suggest that larval release begins in late April, peaks in mid May, and then tapers off, ending by early June (Incze *et al.*, 1987). Zoeae strongly favor surface waters, with approximately 80% being found in the upper 20 m of the water column and > 90% in the upper 40 m (Incze *et al.*, 1987, Fig. 2.2). There is

no evidence of diel migration; depth-specific sampling indicated similar larval depth distributions during day and night (Incze *et al.*, 1987, Fig. 2.2). Following field observations (Incze *et al.*, 1987), we modeled a larval period of two months, capturing the estimated period of the two zoeal stages, which were identically parameterized. We ignored advection during the megalopae stage, as little is known about either the behavior or duration of this life stage, and the spatial scales considered in our study should minimize the influence of additional advection during this stage. However, to test sensitivity of results to this decision, additional analyses were conducted employing a 90-d advection period (Appendix B). Advection during the 90-d period is likely overestimated, given the identical parameterization to the 60-d zoeal period and the likelihood of at least a partial affinity of megalopae for the benthos, which would decrease the proportion of the advection period spent in near-surface waters relative to zoeae.

Rather than applying a fixed number of floats (i.e., larvae) each year, the annual number of floats released varied in proportion to year-to-year changes in reproductive female crab abundance. This allowed us to readily apply our results to a subsequent study of mechanisms associated with interannual variability in recruitment, and it allowed us to explore the potential for additional transport vectors in areas that become relatively more important in years of high reproductive output compared to years of low output. Typically, 5,000-10,000 floats were released per year, with a maximum of 60,232 (1982) and a minimum of 880 (1986) (Fig. 2.3). Apportionment between regions varied with female crab abundance and distributions, but with notable exceptions (1982-1984 in particular), displayed similar trends when considered at the management region level, though the region of west of 166°W longitude tended to receive more floats (Fig. 2.3). The extremely high release number in 1982 is a function of high

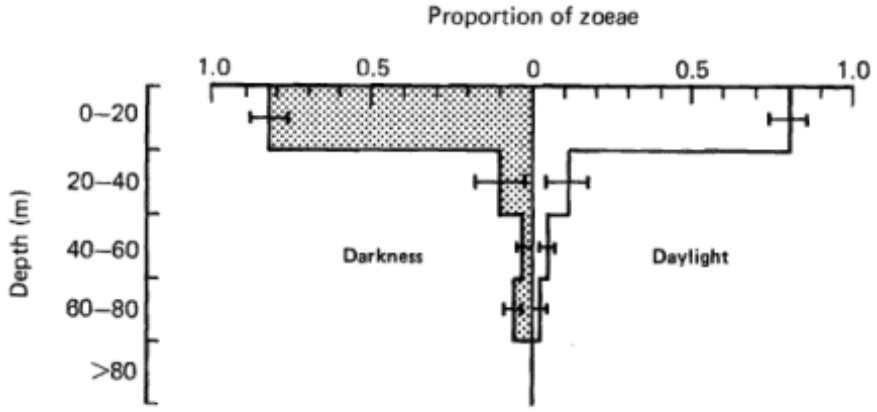

Figure 2.2. Vertical distribution of Tanner crab zoeae. Vertical distribution of stage I and II Tanner crab zoeae by day and night. Note strong similarity of day and night distributions, indicating lack of diel migration (modified from Incze *et al.*, 1987).

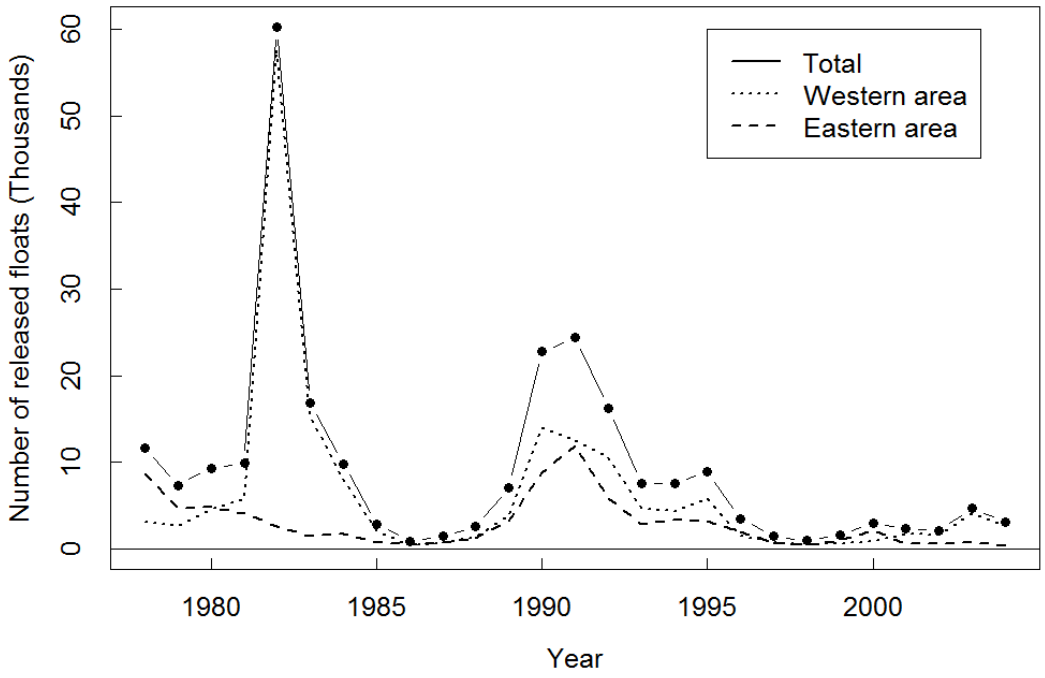

Figure 2.3. Number of floats released by year. Annual count of floats released into the model environment by year east and west of 166° W longitude, and total overall count. Float numbers were set to be proportional to annual abundance estimates of reproductive females.

estimated female abundances for that year due to unusually high densities observed at several survey trawl stations. The spatial and temporal distribution of float releases was determined as follows.

Model floats were released near the center of each NMFS trawl survey station in proportion to estimated annual female densities (crabs/km^2, eq. 2), which were assumed to be representative of female distributions during the spring larval release period. Specifically, to determine the number of floats to be released at a given station, the female density estimate was scaled by dividing by 5 to obtain maximum values within the capabilities of the model, and this value was rounded to the nearest integer. Floats were released uniformly over a period of 10 d for each station. Initial release ranged from April 17th to April 27th, with final release ranging from May 25th to June 6th (Table 2.1). Longer release periods were employed during years with higher female abundances to allow for the likelihood that proportionately more larval crabs hatched in the tails of the hatch timing distribution when abundance is high than when it is low. To mimic the observed distribution of larvae (Incze *et al.*, 1987, Fig. 2.2), floats were released at depths of 10 m (~75% of floats), 30 m (~15% of floats), and 50 m (~10% of floats). Due to a lack of information on vertical behavior of larvae, floats were constrained to remain at constant pressure, that is, remain always at the same depth beneath the free surface. Estimated float locations after 60 d, corresponding to the approximate duration of the two zoeal stages, were considered to represent the model estimated endpoint locations. Model runs were conducted for each year over the period 1978-2004.

Table 2.1. Float release timing. Date of first and final model float releases by year.

Year	First day of release	Final day of release
1978	17-Apr	4-Jun
1979	17-Apr	2-Jun
1980	17-Apr	3-Jun
1981	17-Apr	2-Jun
1982	17-Apr	6-Jun
1983	17-Apr	3-Jun
1984	17-Apr	3-Jun
1985	27-Apr	26-May
1986	27-Apr	22-May
1987	27-Apr	25-May
1988	27-Apr	25-May
1989	17-Apr	2-Jun
1990	17-Apr	6-Jun
1991	17-Apr	4-Jun
1992	27-Apr	26-May
1993	17-Apr	27-May
1994	17-Apr	3-Jun
1995	17-Apr	3-Jun
1996	17-Apr	31-May
1997	27-Apr	25-May
1998	27-Apr	23-May
1999	27-Apr	25-May
2000	17-Apr	27-May
2001	17-Apr	27-May
2002	27-Apr	25-May
2003	17-Apr	2-Jun
2004	17-Apr	27-May

Connectivity

To explore connectivity patterns and source-sink dynamics of EBS Tanner crabs, a connectivity grid was developed representing 27 sub-regions (Fig. 2.4). Cross-shelf (east-west) divisions were based on the EBS shelf domains defined by the 50- and 100-m isobaths and the shelf break. Along-shelf (southeast-northwest) divisions were based on domains similar to those of Parada *et al.* (2010), except that finer subdivisions were used to avoid overestimation of local retention owing to the use of regions that may be too large. To test sensitivity of connectivity results to grid design, an alternative grid was also examined (Appendix B).

Connectivity was calculated as the percentage of floats from a given source region *x* with end points in a given sink region *y*. To explore effects of depth on advection, connectivity was examined at four levels based on the depth at which floats were held: 10 m, 30 m and 50 m, and "bulk", representing all depths together. To allow for examination of long-term trends in addition to trends both before and after the 1989 regime shift (Hare and Mantua, 2000; Rodionov and Overland, 2005), while maintaining roughly equivalent sample sizes in the connectivity time series, annual model runs were divided into two time periods, 1978-1990 and 1991-2004, with a third representing advection patterns over the full (1978-2004) time period. Annual connectivity of one region to another was classified as weak (involving < 10% of floats), moderate (10-30% of floats) or high (> 30% of floats), while the level of consistency in connectivity patterns was judged on the basis of connectivity levels meeting these same criteria in a minimum of 4 yr of each sub-period (1978-1990, 1991-2004) or 8 yr of the full period examined (1978-2004).

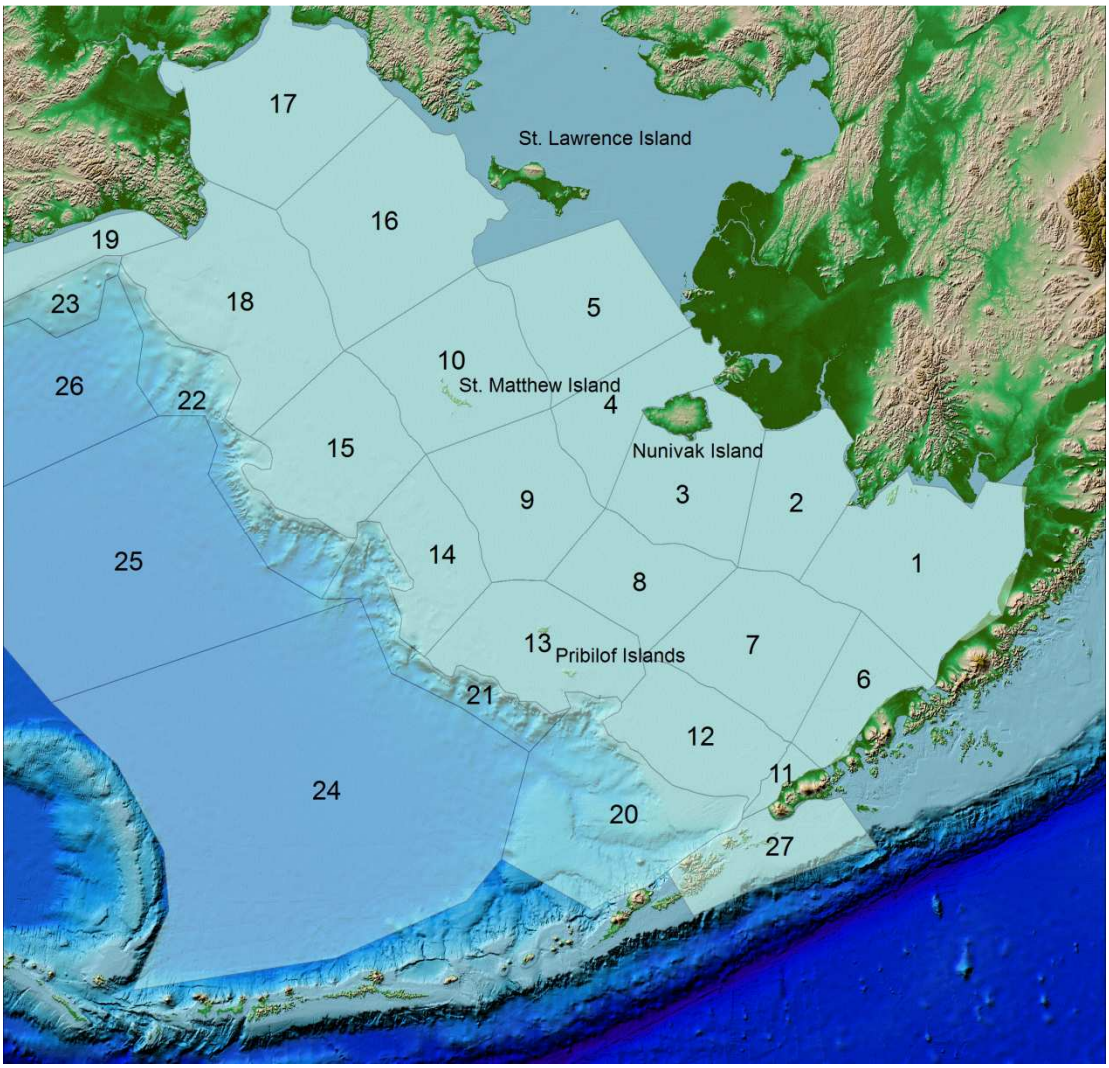

Figure 2.4. Connectivity regions. Map of connectivity regions used in this study. The NMFS annual bottom trawl survey generally corresponds to regions 1-4, 6-10, 11-15, and the southern portion of region 18.

In practice these minimum temporal thresholds were comfortably exceeded, particularly in the cases of both retention categories and the high connectivity category. In addition, sustained connectivity generally accounting for >10% of floats released in a region, but sufficiently erratic as to not clearly fit into any of the previously identified categories, was classed as highly variable. Anomalous advection events were defined as those involving >~5% of the floats released in the source region in at least one year but not in more than 3 yr of either subperiod or not in more than 6 yr of the full period, and not fitting into any distinct pattern. Anomalous advection events were further classified as either minor (< 30%) or major (>30%) events. Typically the maximum temporal threshold for the anomalous classification was not reached, particularly when the full period was considered. Retention was computed as the proportion of floats with endpoints in the source region, and was classified as being either high (30-50%) or very high (> 50%) using similar procedures to those used for connectivity.

Exchange Between Management Subdistricts

To specifically evaluate the current Alaska Department of Fish and Game's (ADF&G's) management strategy of the EBS Tanner crab stock as two substocks, east and west of 166º W longitude, we calculated rates of retention within and advection between the management subdistricts delineated by this boundary. Retention was classified as the percentage of model floats released in subdistrict *x* that remained in subdistrict *x* after 60 d, while advection rates were calculated as the percentage of floats released in subdistrict *x* that were advected more than *z* degrees longitude into subdistrict *y*. Unlike our connectivity analyses, we did not use defined levels of connectivity or retention.

Results

General Transport and Endpoint Patterns

The distribution of female crabs strongly influenced the numbers of float releases in the eastern and western areas (Figs 2.5a, b). The spatial distribution of float endpoints among these two areas mimicked these patterns owing to high rates of retention over these large spatial scales (Fig. 2.5c).

To separate the effect of number of floats (i.e., female spawning abundance, Fig. 2.3) from the effect of advection on model results, the number of model float endpoints was expressed as a percentage of the annual total. Patterns of floats at all depths combined (bulk) exhibited considerable interannual variability, although several interesting trends were observed. High modeled larval endpoint rates occurred within Bristol Bay through the 1980s, but diminished since the early 1990s. Inner Bristol Bay (region 1) accounted for > 20% of all model endpoints in some years; when adjacent regions are included this proportion rises to > 30% (Fig. 2.6a). Substantial numbers of endpoints occurred within the middle domain throughout the entire time period, particularly in the southern and central portions, where region 7 accounted for > 30% of endpoints throughout most of the study period (except 1980-1987) and up to 50% during the mid-1990s (Fig. 2.6b). The southern outer domain (region 12) accounted for a limited number of endpoints through the early 1990s, but increased in importance thereafter (Fig. 2.6c). A major, though highly variable, zone for endpoints occurred in the vicinity of the Pribilof Islands (region 13), particularly since the 1990s (Fig. 2.6d). Finally, a significant endpoint zone occurred southwest of St. Matthew Island (region 15) through the early 1980s, receiving >30% of floats during several years in the 1980-1985 period

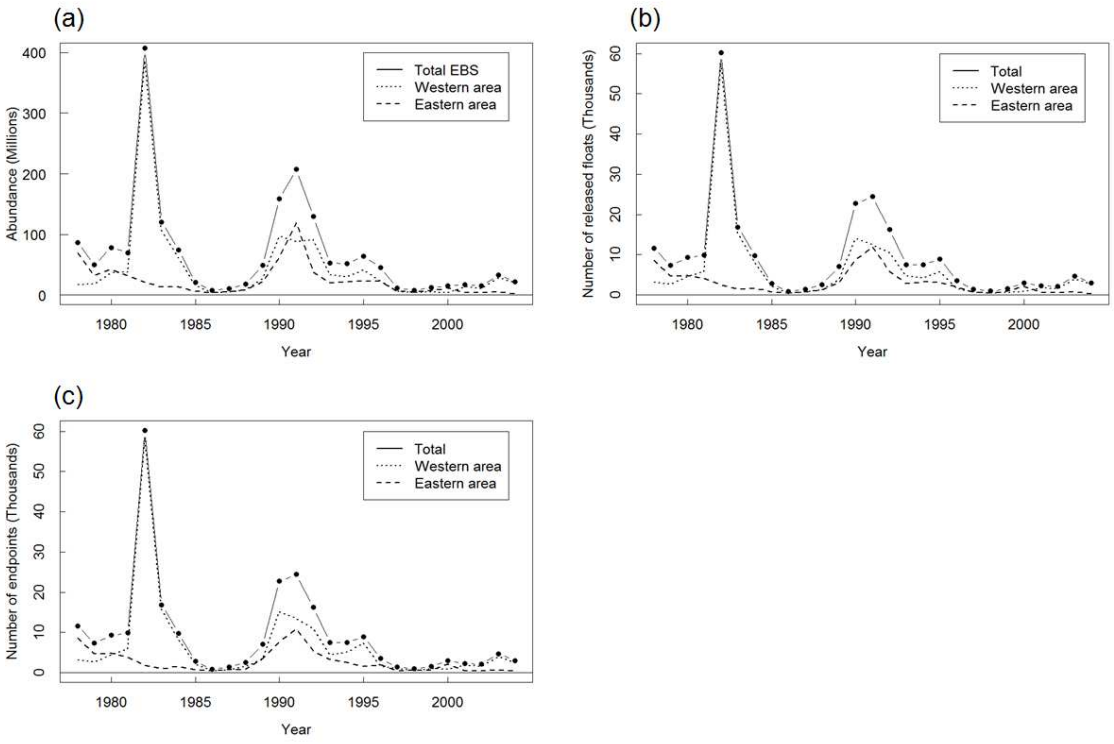

Figure 2.5. Trends in numbers of female crabs and floats. Numbers of (a) reproductive female crabs (b) float releases, and (c) 60-day model endpoints over 1978-2004 that were east (Eastern area) or west (Western area) of 166° W longitude.

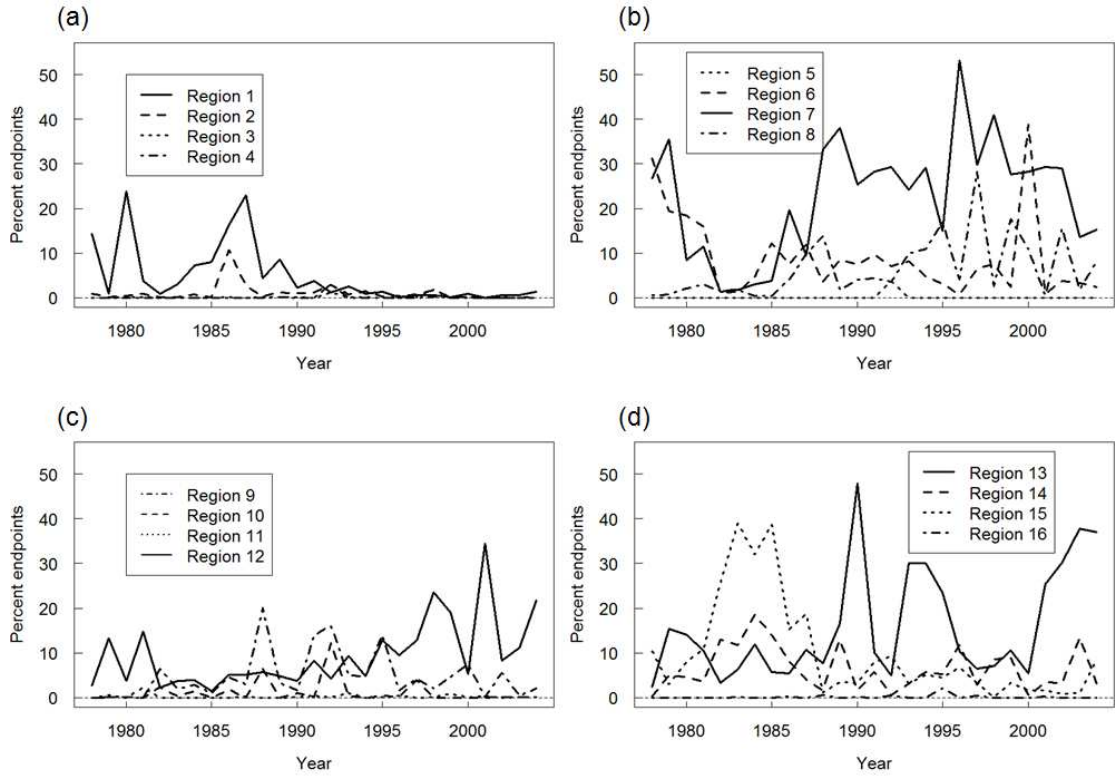

Figure 2.6. Float endpoint trends. Trends in percentages of float endpoints in (a) regions 1-4, (b) regions 5-8, (c) regions 9-12 and (d) regions 13-16. Note trends for region 7 comprising the southern middle domain and region 13, the Pribilof Islands region. Also, note apparent significant settling in region 15 during early 1980s.

(Fig. 2.6d). Endpoint trends were generally robust to an extended advection period (Appendix B).

In addition to these major trends, sporadic advection events carried floats into the Aleutian Basin and to the western and northern Bering Sea shelves, particularly during the late 1970s and early 1980s. However, no more than 30% of floats were advected outside of the Tanner crab survey area on the continental shelf (regions 1-4, 6-15 and the southern portion of region 18) in any year (Fig. 2.7).

Retention

Modeled retention within the overall EBS study region was lowest in the early 1980s, but never < 70% (Fig. 2.7). Retained floats contributed greatly to the total number of float endpoints within a given region, accounting for nearly 100% of endpoints in regions 1, 6, 7, 13, 14, 15 and 18 in at least some years examined (Figs 2.8, 2.9, 2.10). We observed high variability in the proportion of retained floats, with regions 1, 6 and 7 demonstrating strong trends in the contribution of retained floats to estimated endpoints (Figs 2.8a, c and d). The trend in region 6 is noteworthy for being cyclical with retained floats dominating during the mid 1980s and early 2000s, and imported floats dominating in the early 1980s and throughout the 1990s (Fig. 2.8c). Likely due to its upstream position relative to other major source regions, endpoints in region 12 were almost exclusively the result of retention (Fig. 2.9c). Very high (> 50%) bulk float retention occurred in all major source regions, except for region 11 (near Unimak Pass), a small region subject to strong currents (Figs 2.1, 2.4), both of which reduce the probability of retention (Fig. 2.11, Table 2.2). While most regions demonstrated very high retention rates across the full time period, several regions did not. Region 2 (northern Bristol

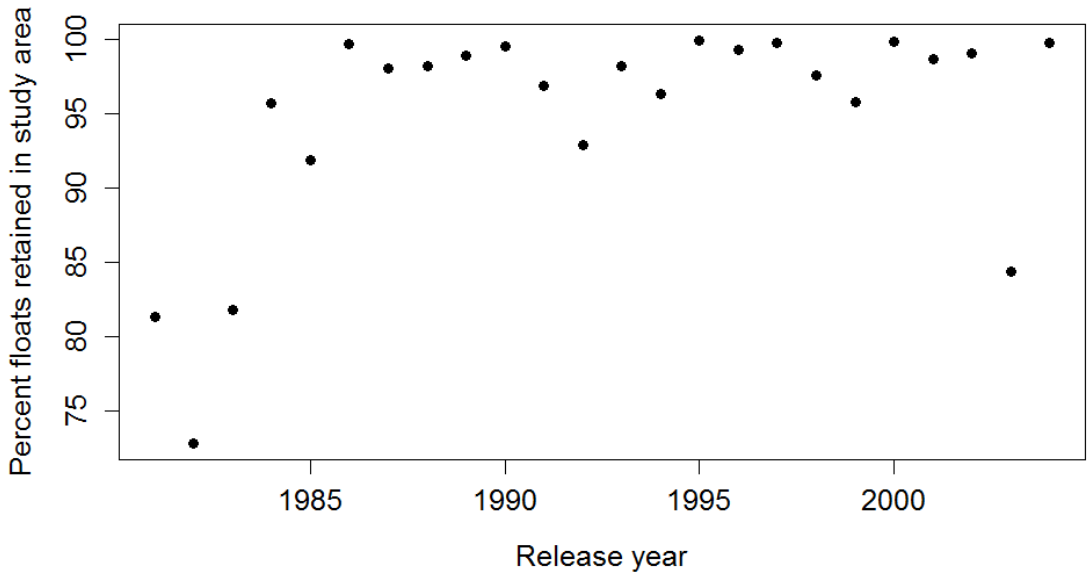

Figure 2.7. Retention within survey area. Annual percentages of floats retained within the eastern Bering Sea (regions 1-4, 6-15 and the southern portion of region 18), corresponding to the area covered by the NMFS survey.

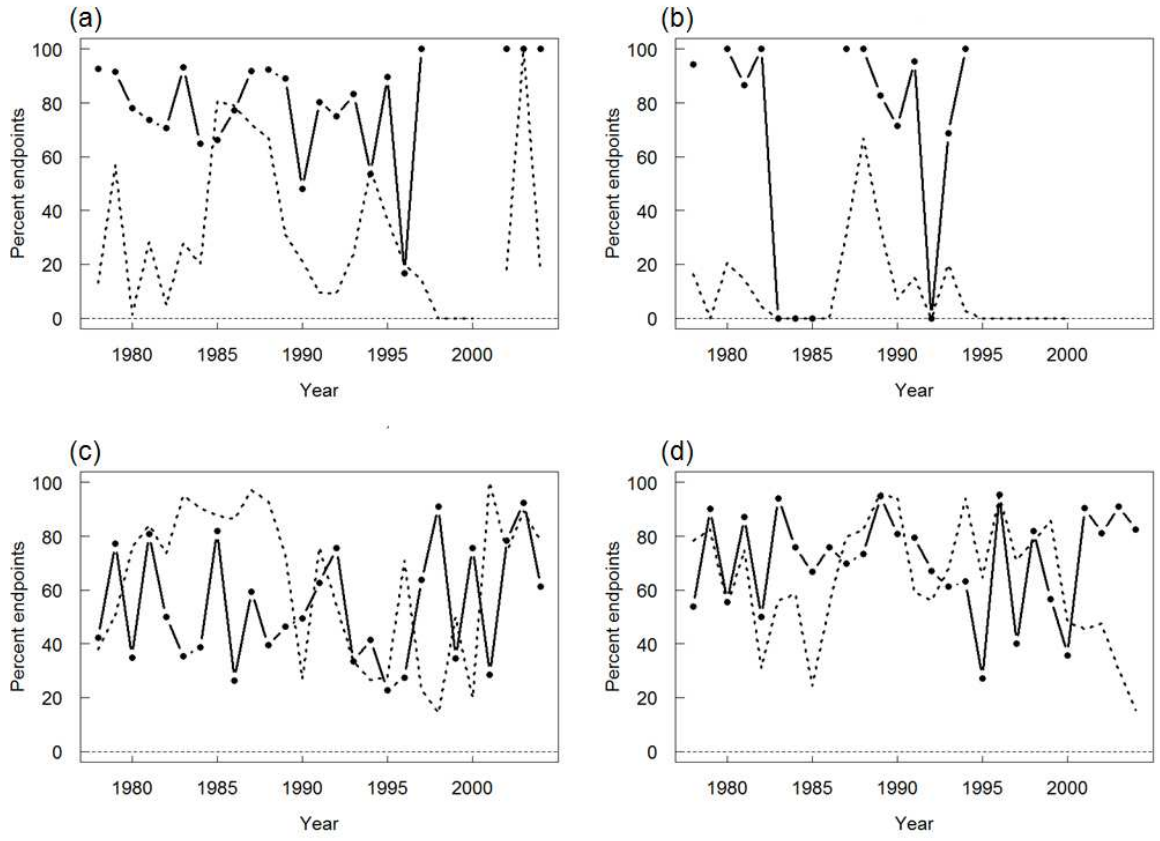

Figure 2.8. Retention dynamics for regions 1, 2, 6 and 7. Trends in percentage of floats originating in a region that were retained in the same region (solid line with points) and percentage of total number floats with endpoints in a region accounted for by retention (dashed line) for Bristol Bay regions (a) 1 (b) 2 (c) 6 and (d) 7. Breaks in lines indicate years in which no floats originated in that region.

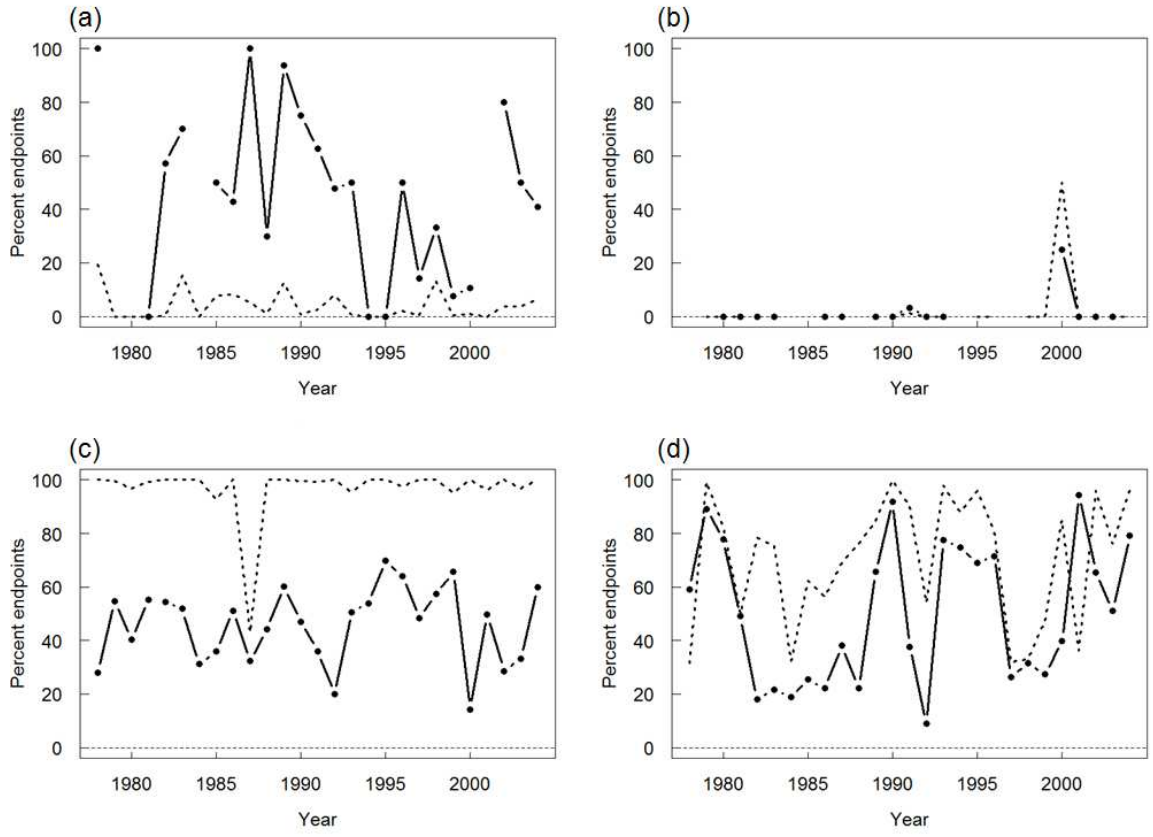

Figure 2.9. Retention dynamics for regions 8, 11, 12 and 13. Trends in percentage of floats originating in a region that were retained in the same region (solid line with points) and percentage of total number floats with endpoints in a region accounted for by retention (dashed line) for Bristol Bay regions (a) 8 (b) 11 (c) 12 and (d) 13. Breaks in lines indicate years in which no floats originated in that region.

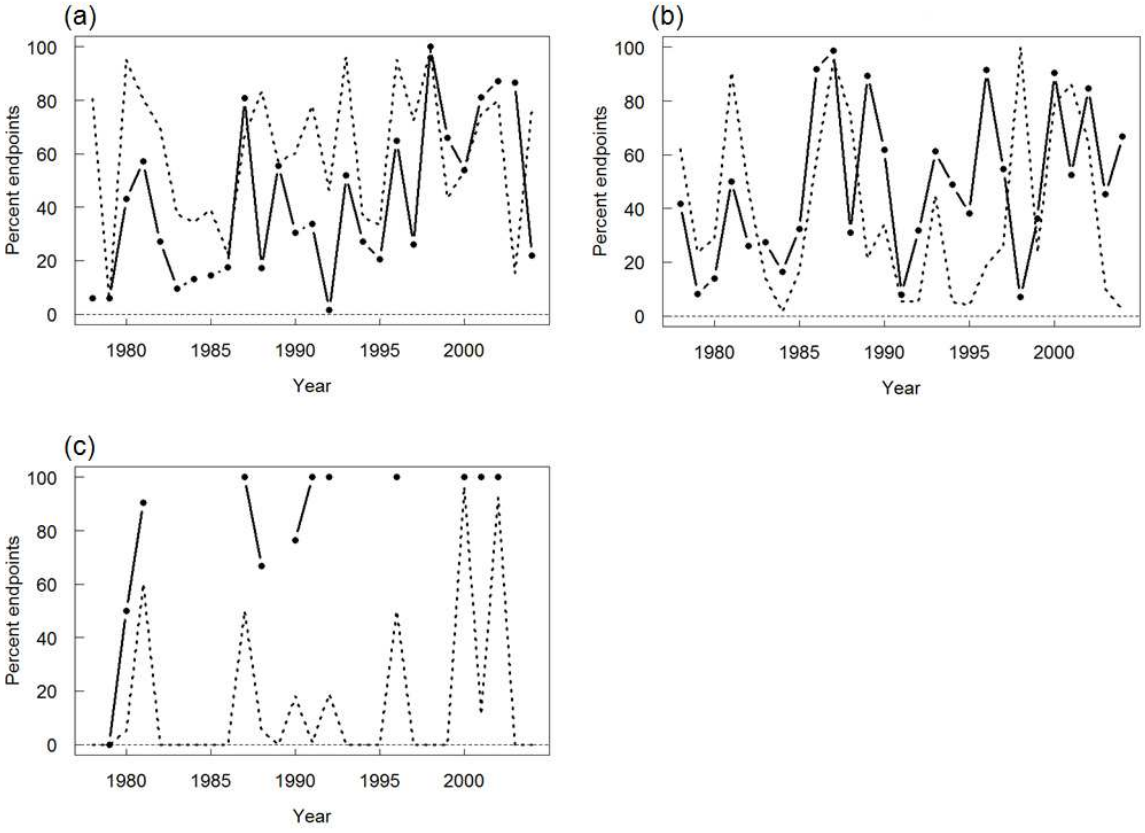

Figure 2.10. Retention dynamics for regions 14, 15, and 18. Trends in percentage of floats originating in a region that were retained in the same region (solid line with points) and percentage of total number floats with endpoints in a region accounted for by retention (dashed line) for Bristol Bay regions (a) 14 (b) 15 and (c) 18. Breaks in lines indicate years in which no floats originated in that region.

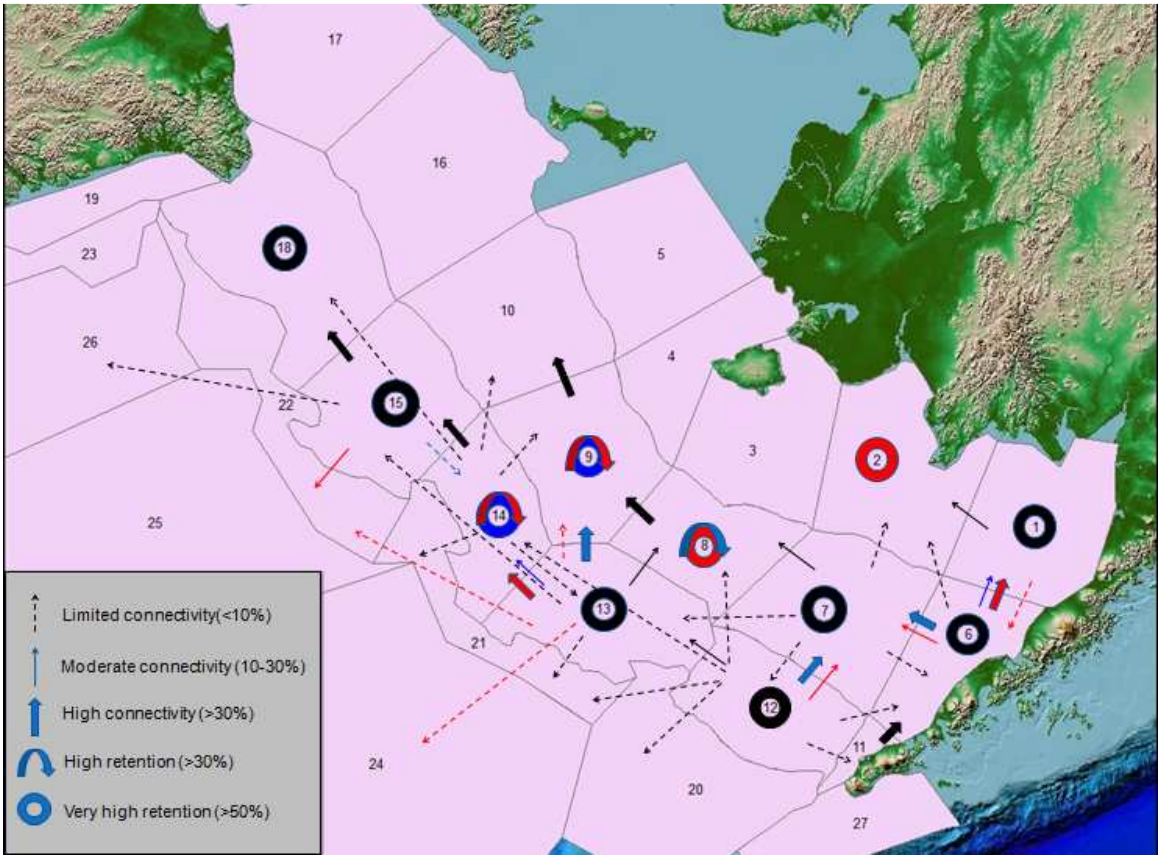

Figure 2.11. Sustained bulk connectivity and retention trends. Trends in bulk long-term retention and connectivity patterns. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004.

Table 2.2. Mean retention rates. Mean retention rates of model floats by region and time period.

Region	1978 to 1990	1991 to 2004	Full period
1	79.20	79.86	79.49
2	66.85	66.02	66.63
3	0.00	33.33	16.66
6	50.95	56.36	53.75
7	74.48	68.07	71.16
8	61.89	34.44	46.38
9	49.10	53.03	51.24
11	0.00	4.03	1.88
12	45.12	46.52	45.84
13	46.10	53.89	50.14
14	29.08	51.60	40.75
15	45.29	51.24	48.38
18	63.92	100.00	81.96
20	0.00	8.33	5.00
22	0.00	0.00	0.00

Bay and Kuskokwim Delta/central inner domain) and region 8 (central middle domain) both had higher retention prior to than after 1990, though for different reasons (Fig. 2.11). In the case of region 2, the local adult population was essentially extirpated following the early 1990s population crash and has not recovered (Fig. 2.8b), thus this region had no floats released within it after that time. For region 8, reduced retention following 1990 was associated with a number of anomalous advection events to surrounding regions (Fig. 2.12).

Conversely, regions 9 (northern middle domain), 13 (central outer domain/Pribilof Islands) and 14 (northern outer domain) experienced higher retention rates following 1990 (Table 2.2). In region 9, increased retention was associated with a reduction in anomalous advection events, which had led to significant export of floats to surrounding regions during the 1980s, particularly region 14 (Fig. 2.11 and 2.12). Interestingly, region 13 demonstrated a cyclical pattern in retention (not shown), with a period of reduced retention (~20-40%) occurring from 1982-1988, followed by a large increase in retention (75-90%) during the early 1990s. Subsequently, a second, shorter duration and less dramatic period of reduced retention occurred during 1997-2000, followed by a second increase after 2000. Periods of increased retention were associated with decreased connectivity with regions 14, 15 and 22 (1990s) and a cessation of onshore advection to regions 8 and 9 (post-2000). Finally, for region 14, decreased retention prior to 1990 was associated primarily with minor anomalous advection events to regions 9, 10 and 21 (Fig. 2.11, and Fig. 2.12). The pronounced trends in interannual variability in retention suggested by bulk float analyses were also evident in analyses of floats by depth, particularly at 10 and 30 m depth (Figs 2.13 and 2.14). However, retention rates increased notably at greater depths; for instance, at 50 m all source regions, with the exception of region

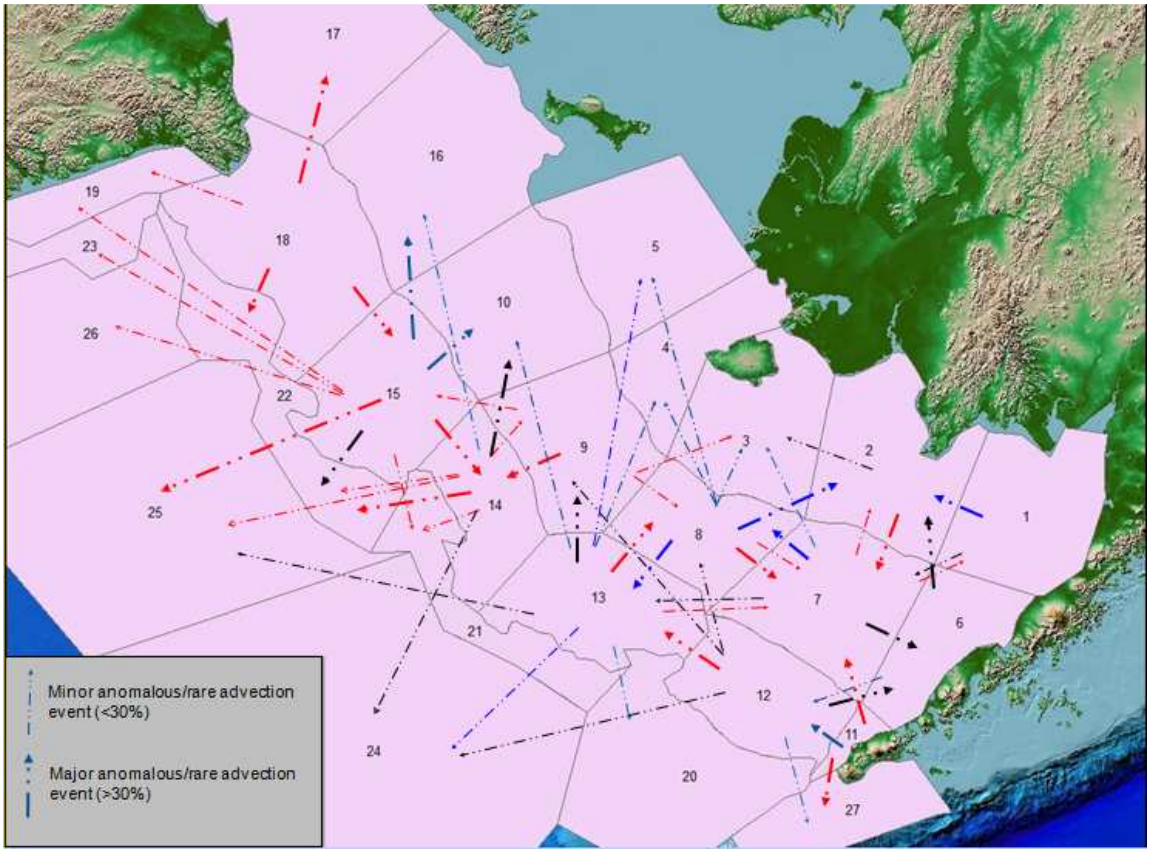

Figure 2.12. Bulk anomalous transport events. Trends in bulk anomalous advection events (1 to 3 events in a sub-period or 1 to 6 events during full period of study), color coded by time period of occurrence. Black denotes events occurred across full time period (1978-2004), red indicates that events were only observed during 1978 to 1990, and blue indicates that events were observed during1991-2004 only.

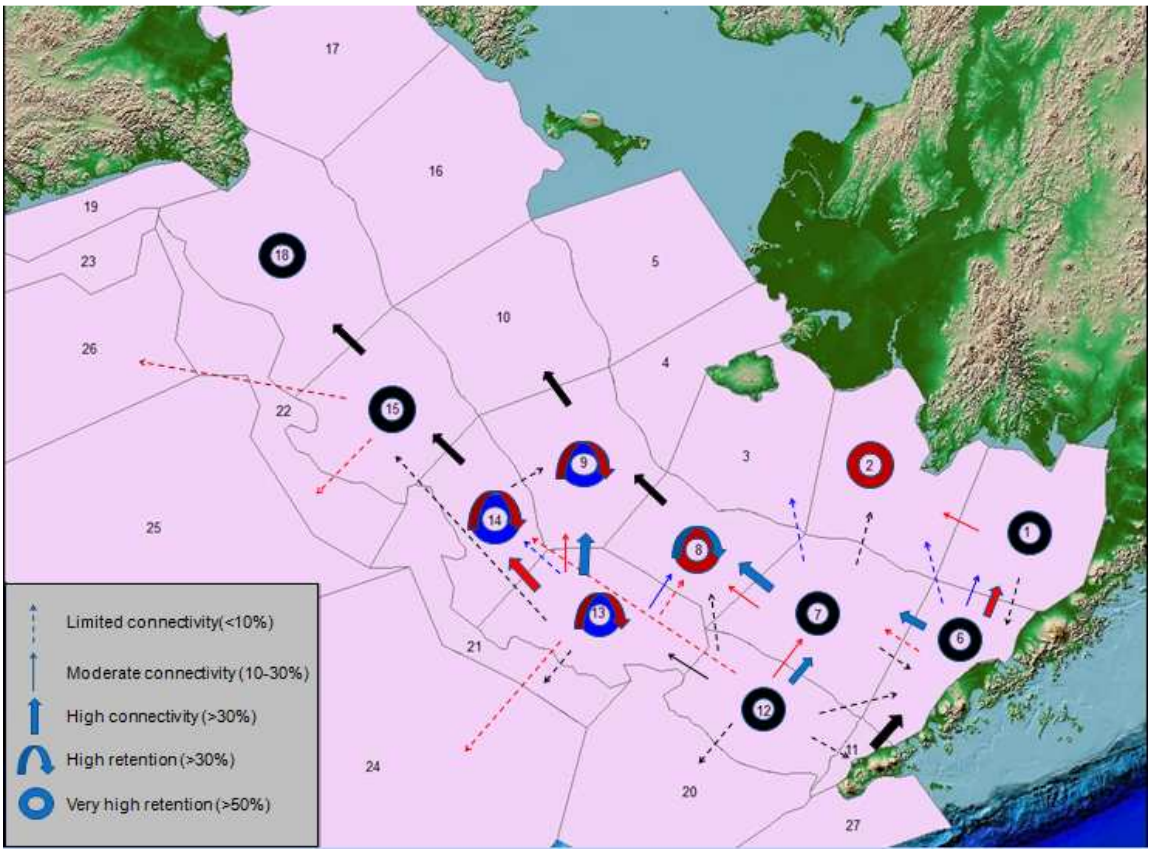

Figure 2.13. Sustained connectivity and retention trends at 10 m. Non-anomalous connectivity and retention trends at 10 m depth. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004.

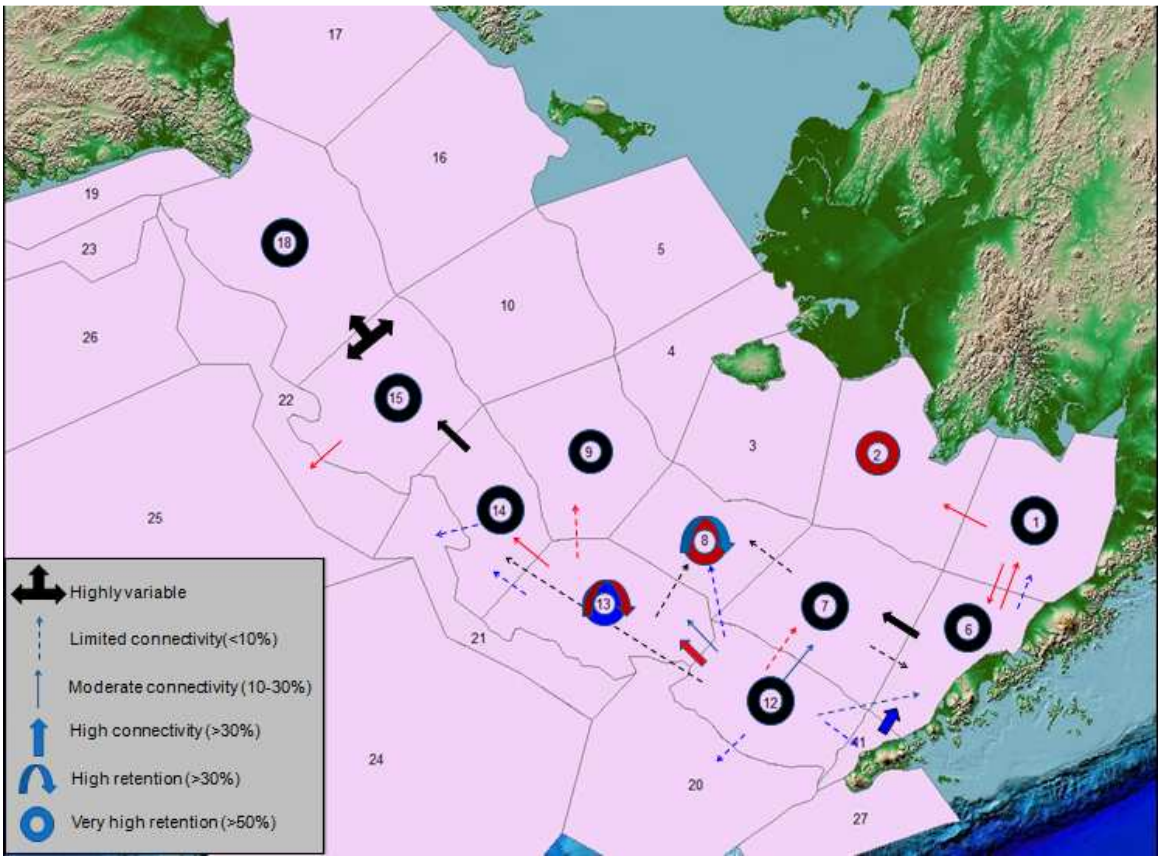

Figure 2.14. Sustained connectivity and retention trends at 30 m. Non-anomalous connectivity and retention trends at 30 m depth. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004.

11, experienced very high (>50%) retention (Fig. 2.15). An extended (90-d) larval period had relatively limited effects on retention trends, with the most pronounced being reduced retention in the regions of the outer domain during the 1980s, which strengthened during the 1990s (Appendix B). Retention trends in the regions of the middle and inner domains were not notably altered.

Connectivity

The number of connections between regions increased with both the number of floats released annually and the number of regions in which floats were released (Table 2.3). Maximum number of connections (60) was not however observed at the highest numbers of released floats, but occurred in 1981 with a release of 9,481 floats, somewhat less than the average number of floats released (10,023). Increases in number of connections were accounted for by anomalous events, and events involving too few floats to be classified by our criteria. High rates of along-shelf advection were evident in both the middle and outer domains, with the predominate direction being to the northwest (Fig. 2.11). In the central and northern portions of the middle domain (regions 8, 9 and 10) and outer domain (regions 13, 14 and 15), high connectivity levels (>30%) were predominately observed in this direction (Fig. 2.11). Concurrent with observed ocean current patterns, southeasterly advection was much weaker, being most prevalent during anomalous events, although weak long-term southeasterly advection trends were indicated from region 7 to 6 and from region 15 to 14 (Figs 2.11 and 2.12).

While weak offshore advection was observed in the southern portions of the middle and outer domains, from region 7 to 12, sustained cross-shelf advection was limited compared to

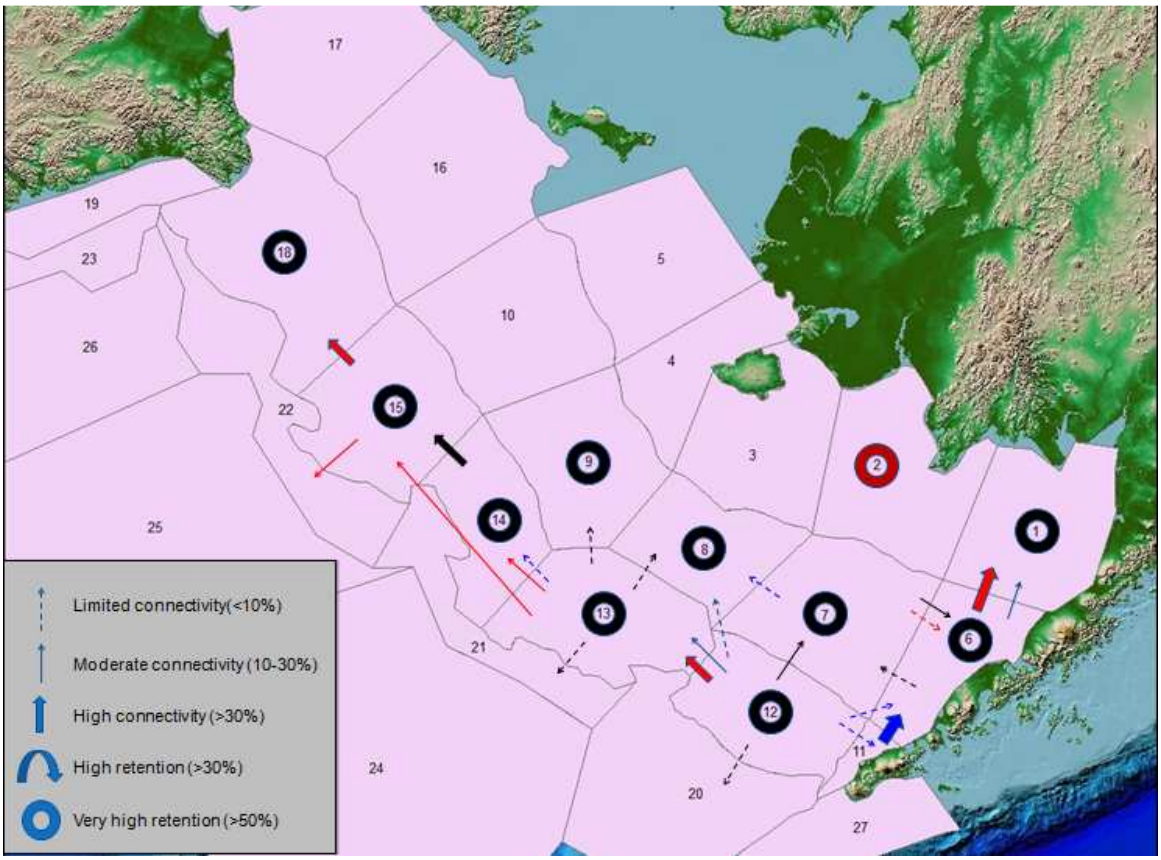

Figure 2.15. Sustained connectivity and retention trends at 50 m. Non-anomalous connectivity and retention trends at 50 m depth. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004.

Table 2.3. Trends in interregional connections and covariates. Number of floats released annually, number of annual interregional connections, and number of regions in which float start locations occurred.

Year	Number of floats	Number of connections	Number of start regions
1978	11653	42	10
1979	7288	38	9
1980	9292	44	10
1981	9841	60	12
1982	60232	50	12
1983	16826	49	11
1984	9795	43	9
1985	2871	34	10
1986	880	32	9
1987	1411	35	13
1988	2517	43	11
1989	7037	45	12
1990	22763	51	13
1991	24396	53	12
1992	16253	58	13
1993	7531	53	11
1994	7543	35	9
1995	8924	37	8
1996	3471	39	10
1997	1409	31	8
1998	943	29	8
1999	1552	36	8
2000	2974	31	9
2001	2309	33	9
2002	2074	28	11
2003	4710	42	11
2004	24126	32	10

along-shelf patterns, with the primary direction being onshore (Fig. 2.11). Onshore connectivity between region 12 and region 7 varied over time; prior to 1990 only a moderate level of connectivity was present, while following 1990 connectivity became strengthened, such that after 2000 floats originating in region 12 comprised the majority of those with estimated endpoint locations in region 7 (Fig. 2.16). The reverse occurred for onshore exchange between region 6 and region 1; connectivity was highest prior to 1990 but weakened afterward, being offset by strengthened advection from region 6 to region 7 (Fig. 2.11). Despite weaker connectivity, floats originating in region 6 continued to account for a majority of estimated endpoints in region 1 (Fig. 2.17)**.** Finally, high rates of onshore advection occurred between region 11 and region 6 throughout the study period (Fig. 2.11).

Patterns in both moderate connectivity (10-30%) and weak connectivity (<10%) displayed some similarity to those for high connectivity, however notable differences were observed. Within the outer domain a significant northwesterly vector was also apparent in moderate-strength connectivity, while onshore advection was a much more pronounced component at this level of connectivity (Fig. 2.11). Offshore advection was also notable, particularly for region 15, which demonstrated moderate connectivity with adjacent regions of both the shelf (region 22) and north-central Aleutian Basin (region 25) during the 1980s (Fig. 2.11). The direction and distance of weak connectivity trends were more variable than either the significant or moderate categories. Within the inner domain, advection within this category was predominately towards the northwest (Fig. 2.11). Conversely, depending on the source region in question, cross-shelf advection within the middle domain was either onshore or offshore, while along-shelf advection may be to the north or to the south, demonstrating this

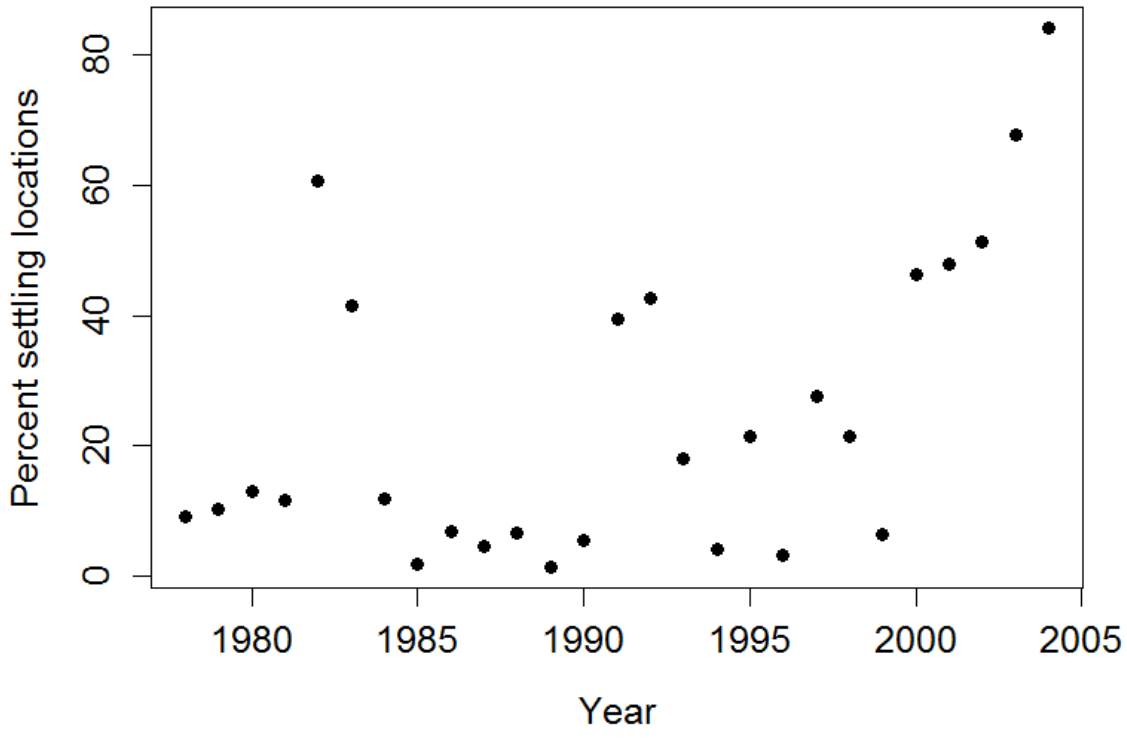

Figure 2.16. Contribution of region 12 to endpoints in region 7. Trends in the percentage of total endpoints in region 7 accounted for by floats originating in region 12.

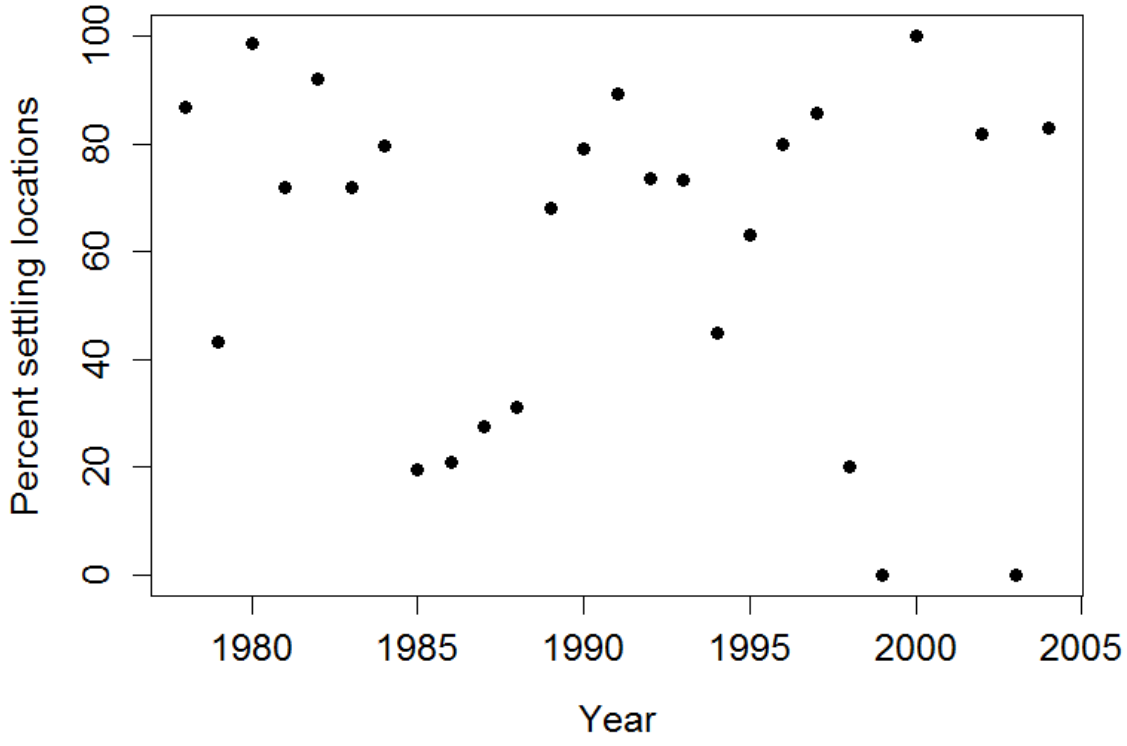

Figure 2.17. Contribution of region 6 to endpoints in region 1. Trends in the percentage of total larval endpoints in region 1 accounted for by floats originating in region 6.

region's general lack of a defined current pattern (Fig. 2.11). Despite having a comparatively well-defined current system, similar trends are also observed within the outer domain, with notable offshore-directed connectivity occurring with both the continental slope and the Aleutian Basin (Fig. 2.11).

In comparison to these results for the standard 60-d advection period, connectivity trends using the custom grid were not greatly affected by an extended 90-d advection period, with only trends at the limited scale being notably different (Appendix B). Advection patterns at 10 m largely reflected bulk advection patterns, likely due to the fact that floats released at this depth comprised the majority of all floats released (Fig. 2.13). However, advection within the middle domain (regions 7-9) and middle/northern outer domain (regions 13-14) was markedly reduced at a depth of 30 m (Fig. 2.14). The magnitude of advection further decreased at 50 m depth, with one exception: an increase in the proportion of floats released at that depth in region 6 transported to region 1 was observed at 50 m during the 1980s (Fig. 2.15). With increasing depth, limited connectivity trends became a prominent advection feature, particularly within the middle domain, and between the outer and middle domains as advection patterns weakened (Figs 2.14 and 2.15). Further, persistent advection from the middle to the outer domain ceased; the only offshore advection observed was at the anomalous event level (Figs 2.14 and 2.15).

Anomalous Advection Events

Anomalous advection events were, by definition, highly variable. Offshore advection from the outer domain to the Bering Sea basin is a notable feature within this category, in addition to advection to both the northern and western Bering Sea continental shelves (Fig.

2.12). An apparent shift occurred in anomalous events originating in the outer domain after 1990; a stronger trend in offshore advection was apparent before 1990, afterwards, onshore advection became more prevalent (Fig. 2.12). Anomalous advection at specific depths was variable with few observable trends; offshore advection from the outer domain during the 1980s was prevalent at 10 m and 30 m depth, but not at 50 m, while onshore advection during the 1990s was a feature at 10 m. Additionally, within Bristol Bay anomalous advection from region 1 to regions 2, 6 and 7 occurred during the 1990s. Finally, anomalous events became the primary means of advection from the middle domain to the outer domain when depth classes were considered separately; persistent connectivity observed at the bulk level was supported by combined anomalous advection across multiple depth ranges.

Exchange Between Management Subdistricts

Cross-shelf advection between domains in terms of both number of floats advected and distance covered was of limited magnitude, as reflected in high rates of retention within both eastern and western subdistricts (Figs 2.18a and 2.19a) and relatively low advection rates between subdistricts. Advection from the eastern to the western subdistrict was primarily related to northwestward advection in the southern middle and outer domains, and connectivity between regions 7 and 12 (Figs 2.11, 2.18b, c and d). The magnitude of this advection, however, declined rapidly with increasing distance (Fig. 2.18). Advection from the western to the eastern subdistrict was much more limited, suggesting that, while the western subdistrict may receive significant larval subsidies from the eastern substock, the reverse is not typically the case (Fig. 2.19a). For floats released in the western subdistrict, advection rates to greater than 1 degree longitude east of 166º W were typically under 10%, except for several strong

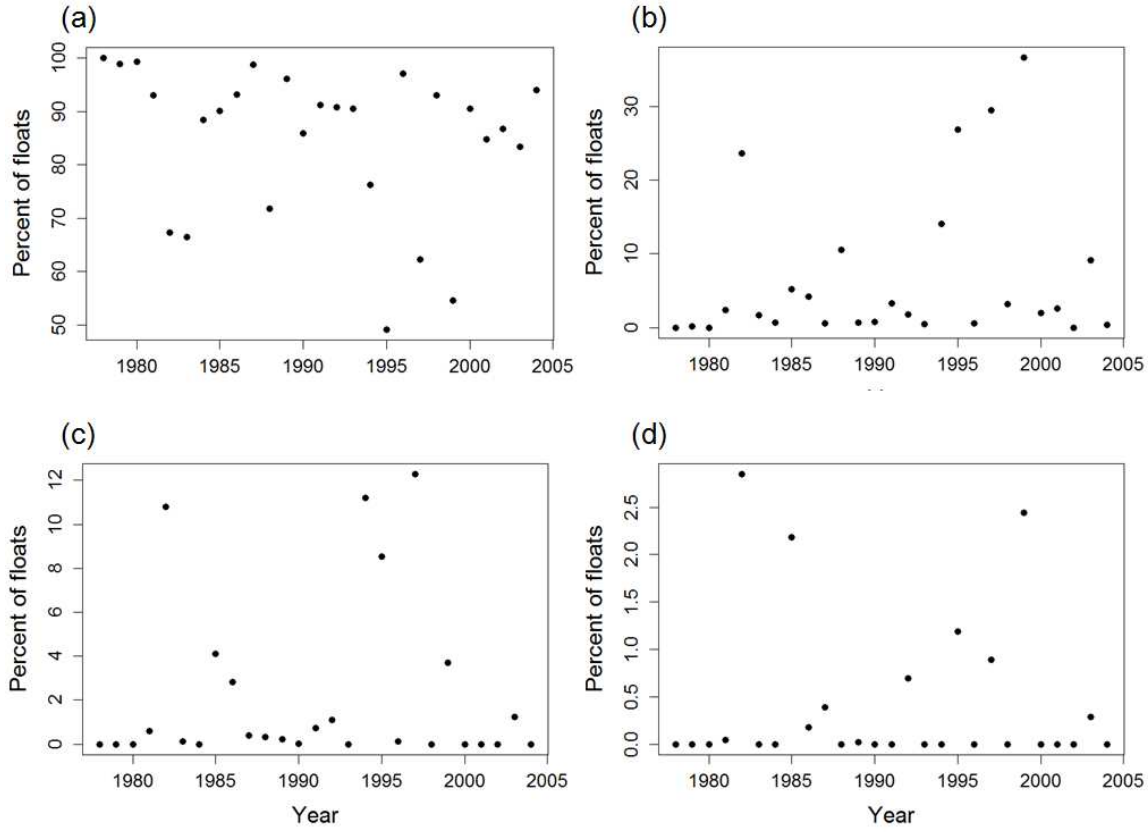

Figure 2.18. Trends for floats released in the eastern subdistrict. The fate of floats released in the eastern subdistrict in terms of rates of: (a) retention in eastern subdistrict, (b) advection more than 1º longitude west of 166º W, (c) advection more than 2º longitude west of 166º W, and (d) advection more than 3º longitude west of 166º W.

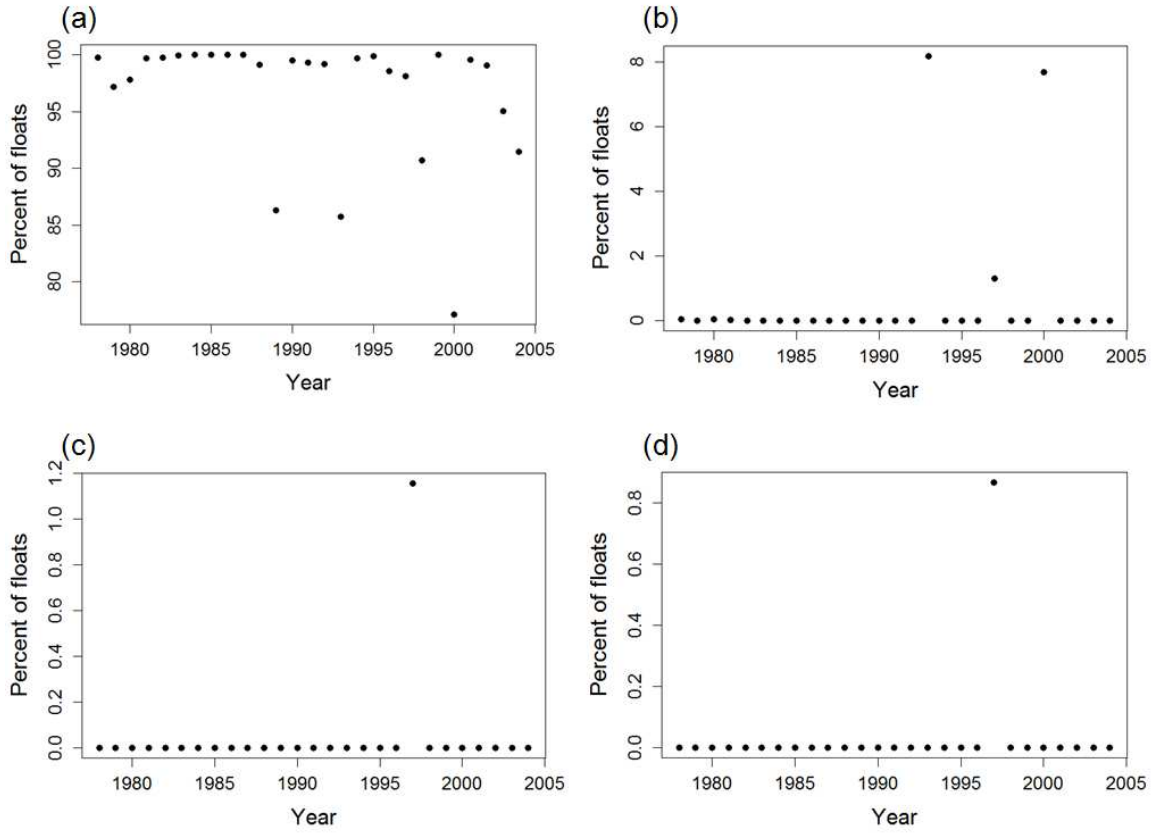

Figure 2.19. Trends for floats released in the western subdistrict. The fate of floats released in the western subdistrict in terms of rates of: (a) retention in western subdistrict, (b) advection more than 1º longitude east of 166º W, (c) advection more than 2º longitude east of 166º W, and (d) advection more than 3º longitude east of 166º W.

anomalous events occurring primarily in the mid 1990s (Fig. 2.19b). For advection over distances greater than 2^{o} longitude, even these events were greatly diminished in magnitude (Figs 2.19c and d).

Discussion

We used a state-of-the-art ROMS model to investigate whether EBS Tanner crabs comprise a single metapopulation with spatial subunits that are well interconnected by larval advection and whether larval settling patterns reflect large-scale population trends. Our results support the hypothesis that the EBS Tanner crab metapopulation may be comprised of multiple subunits within which retention is an important component of recruitment, but which are connected by limited exchange of larvae.

Broad regional patterns in model float settlement were very closely related to the distribution of float releases that mimicked the density distributions of reproductive female crabs. This suggests to us that female abundance and distribution is the most important factor driving changes in the relative abundance of the stock in the Bristol Bay and Pribilof Islands areas over the long term. To distinguish trends in float retention and connectivity from these patterns in female abundance, the percentages of the floats released in the given region that were retained (relative retention) or advected to another region (relative connectivity) were used.

Northern Bristol Bay (region 2) appeared to be most isolated, with very limited advection of larvae from only two adjacent regions (inner and middle Bristol Bay). More broadly, the southeastern Bering Sea (regions 1, 2, 6, 7, 12) received very limited larval subsidies from other EBS regions, and thus appears to be highly reliant on retention from a

self-sustaining local metapopulation subunit. This contrasts with the central and northern regions of both the middle domain (regions 8 and 9) and outer domain (regions 13 and 14) where recruits may represent local retention plus advection predominately from the southeast. Furthermore, the prevalence of estimated endpoint locations in region 7 after 1988 (25-50%, Fig. 2.6b) suggests that processes within this region may have been of particular importance to recruitment dynamics of both the Tanner crab stock as a whole, and particularly to the southeastern Bering Sea subunit during this period. Interestingly, in region 6, the proportion of endpoint locations contributed by retained floats displayed a cyclical pattern similar to that observed in residuals derived from stock-recruit models for the EBS Tanner crab stock which were based on abundance estimates of reproductive females and small juvenile crabs (Richar and Kruse, in review). Retained floats contributed most during years of apparent strongest recruitment across the EBS, and least in years associated with the weakest EBS-wide recruitment, during which floats originating in regions 7 and 12 predominated. This cycle likely results from changes in the relative distributions of spawning females associated with abundance trends**.** Over the whole area occupied by surveyed Tanner crabs, modeled retention within the population was generally >95%. The lowest retention rates (73-82%) occurred in the early 1980s when Tanner crabs were most abundant and covered the largest geographic area within the region of the trawl survey (Zheng and Kruse, 2006). It is reasonable to assume that larvae that are either advected northward into the northern Bering Sea or offshore into the Aleutian Basin (i.e., beyond the extent of the NMFS survey) are unlikely to survive, due to unsuitable post-settlement habitat and the lack of adult Tanner crabs in those areas.

Consequently, retention within the EBS region as a whole does not seem likely to comprise a determinant of recruitment to the adult population.

Our finding that the southeastern Bering Sea could be considered as a reproductive subunit of the EBS Tanner crab metapopulation could be construed to be consistent with published genetic differences between Tanner crabs from Bristol Bay and those collected in the vicinity of the Pribilof Islands using allozymes (Merkouris *et al.*, 1998). However, a more recent analysis of those same data using the program STRUCTURE (Pritchard *et al.*, 2000) failed to detect differences (Stewart Grant, Alaska Department of Fish and Game, pers. comm.). Nevertheless, as the number of polymorphic loci was not large, the power of STRUCTURE to detect fine-scale population structure may be marginal. This potential contradiction may also be explained as the result of periodic low levels of long-distance larval advection and anomalous events preventing strong, consistent genetic differentiation through genetic exchange between substocks, while being sufficiently limited in scale as to not appreciably alter local recruitment dynamics.

Mitochondrial DNA suggests genetic exchange of Tanner crabs along the southern Alaska Peninsula northward into the EBS (Bunch *et al.*, 1998). We observed advection of some EBS floats in the opposite direction. Whereas net flow through the passes is northward, ocean current reversals may occur and southward flow is common on the western side of the passes (Stabeno *et al.*, 2005). It was beyond the scope of our study to examine potential connectivity among Tanner crabs from the Gulf of Alaska and EBS so we did not conduct ROMS analyses with larvae hatched from female Tanner crabs in the Gulf of Alaska. However, in a ROMS analysis of northern rock sole *(Lepidopsetta polyxystra)* larvae spawned in the Gulf of Alaska

just east of Unimak Pass were advected through the pass into the EBS, largely continuing along the 100 m and 200 m isobaths, or to the southwest along the Alaska Peninsula (Lanksbury *et al.*, 2007). Northern rock sole have a shallow vertical distribution very similar to Tanner crab. Similar findings resulted from a study examining advection of larval rockfish, with simulated larvae released near Unimak Pass being advected deep into the EBS by the persistent currents within the outer domain (Stockhausen and Hermann, 2007).

Multiple previous studies have challenged common assumptions about the importance of larval advection vs. retention of local larval production (Becker *et al.*, 2007; Jones *et al.*, 2005; Nahas *et al.*, 2003; Pineda *et al.*, 2007; Sponaugle *et al.*, 2002). In our study, the apparent importance of larval retention contrasts with former statistical evidence that northeasterly winds were associated with stronger Tanner crab recruitment, purportedly owing to offshore advection carrying larvae away from nearshore areas of unfavorable coarse sediments to more favorable offshore habitats comprised of fine sediments where young crabs can bury to reduce predation risk (Rosenkranz *et al.*, 1998, 2001). If northeasterly winds instead foster offshore retention rather than onshore to offshore advection, then these studies can be reconciled with our findings. Annual NMFS trawl survey data reveal that spatial distributions of mature and small juvenile female Tanner crabs overlap, but small immature females tend to favor deeper waters near the continental shelf edge and extending onto the continental shelf whereas mature females extend more from the shelf edge and eastward into shallower waters (Otto and Pengilly, 2002; Zheng and Kruse, 2006). These patterns led Otto and Pengilly (2002) to hypothesize that immature Tanner crabs undergo an ontogenetic migration from deep to shallow water, but this hypothesis has not yet been fully tested. Contrary to those observations,

in the course of conducting our analyses, we observed a generally southwestern, offshore shift in the centers of female crab distribution with ontogeny from the 30-50 mm carapace width size interval to the primiparous stage and then to the first-year multiparous stage (Appendix D).

Advection appears to play an important role in the life history of two other commercially important EBS crab species: Bristol Bay red king crab and EBS snow crab (Zheng and Kruse, 2006). Subsequent to hatching from clutches brooded by mature females in relatively deep, offshore waters of Bristol Bay, red king crab larvae seem to be advected toward shore and into inner Bristol Bay where young crabs occupy shallow-water habitats in association with rocks, shell hash, and biogenic structures (Armstrong *et al.*, 1993). With ontogeny, king crabs move offshore to deeper waters and are thought to migrate in a southwesterly counternatant direction (Armstrong *et al.*, 1993; Zheng and Kruse, 2006).

In contrast, snow crabs are more broadly distributed over the middle and outer domains of the EBS continental shelf, but are not very abundant in Bristol Bay. Using an individual-based model (IBM) coupled to an earlier version of ROMS than used in our study, predicted settlement regions matched observed distributions of immature crabs generally found at the northern-most shallow water stations in the annual NMFS bottom trawl surveys (Parada *et al.*, 2010). With ontogeny, snow crabs appear to migrate in a southwesterly direction toward the continental shelf edge (Ernst *et al.*, 2005; Zheng *et al.*, 2001). In their IBM analysis, Parada *et al.* (2010) suggested the existence of southeast and northwest subsystems within which life cycle closure may occur. However, connectivity of these subsystems appears to be asymmetric with larval export from the southeast to the northwest, but not vice versa. This asymmetry agrees with our findings for Tanner crabs in the southeastern Bering Sea versus the central to

northern portions of the middle and outer domains, and is consistent with the predominant northwesterly flow of currents on the continental shelf (Stabeno *et al.*, 1999).

We also found evidence that variable rates of retention and connectivity may help explain decadal population trends. In particular, modeled float retention in the Bristol Bay region was very high in the 1970s and 1980s in northern Bristol Bay (region 2) and central middle domain (region 8) in the 1970s and 1980s but low since the 1990s. On the other hand, retention increased after 1990 in the northern middle domain (region 9) and central/northern outer domains (regions 13 and 14). Moreover, advection away from the Pribilof Islands area (region 13) north (region 14) declined after 1990, further increasing larval retention in the Pribilof Islands area. These model findings are broadly consistent with survey observations and commercial fishery data. Annual NMFS surveys caught very few Tanner crabs in northeastern Bristol Bay since 1992 (Zheng and Kruse, 2006) and reveal that distribution centers of female Tanner crabs in Bristol Bay have shifted southwest over time (Zheng, 2008). Likewise, fishery production shifted significantly with 86% of EBS Tanner crab landings in weight taken from the Bristol Bay area during the 1970s and 1980s and only 41% taken from this same area in the 2000s (Fitch *et al.*, 2012).

Specific mechanisms for the observed geographic shift in larval retention around 1990 remain uncertain, though we speculate that they may be related to the 1989 regime shift. Since 1990, there has been increased winter cooling of the coastal waters in the Bering Sea, an intensification of the winter and summer Arctic Oscillation (AO), and a weakened winter Aleutian Low (Hare and Mantua, 2000). Among the indices considered by Rodionov and Overland (2005), the 1989 regime shift was most clearly indicated by the Arctic Oscillation

(AO) index, which may have contributed to cooling in the Bering Sea after an exceptionally warm period, which began in 1977 (Rodionov and Overland, 2005). A number of ecological changes occurred in the EBS consistent with the 1989 regime shift (Hare and Mantua, 2000; Rodionov and Overland, 2005). Among them, recruitment variability in several species of EBS groundfish has been linked to changes in decadal scale variability in both the Aleutian Low and the Arctic Oscillation (Wilderbuer *et al.,* 2002). Further, jellyfish biomass increased sharply in the 1990s (Brodeur *et al.*, 2002) concurrent with a redistribution of jellyfish biomass from the southeastern Bering Sea along the Alaska Peninsula in the 1980s toward the northwest to the middle shelf domain and deeper waters including the Pribilof Islands area (Brodeur *et al.*, 2002). The similar shifts in geographic distributions of both jellyfish and Tanner crab larvae are intriguing.

High rates of retention of modeled Tanner crab larvae may provide some clues about population regulating mechanisms for this species. Tanner crabs are cannibalistic, with larger crabs feeding on smaller individuals (Jewett and Feder, 1983). Because regions with higher crab densities account for greater annual larval production, high levels of retention may support a hypothesis that juvenile recruitment is regulated by cannibalism by older, larger conspecifics. In a semi-enclosed fjord (Glacier Bay, Southeast Alaska) juvenile Tanner crabs were found over the full range of depths sampled (15–439 m), but they were most abundant <150 m where adults were rare (Nielsen *et al.,* 2007). This spatial segregation led Nielsen *et al.* (2007) to conclude that cannibalism may be important in structuring that population. Such a mechanism could explain a strong negative relationship between survival, measured as the natural

logarithm of recruits per mature female, and mature female abundance (Richar and Kruse, in review).

Development of an IBM for Tanner crab akin to Parada *et al.* (2010) has the potential to provide more realistic model results, though a number of data limitations should first be addressed. In conducting our own analyses, we were hampered by the limited state of current knowledge regarding Tanner crab behavior and physiology during the larval and juvenile stages. Of particular concern is the potential for larval vertical movements, either diurnal or tidally driven, as such movements will lead to errors in estimated advection and retention rates (Sponaugle *et al.*, 2002). Although Incze *et al.* (1987) found no evidence for diurnal movement, this conclusion was based on limited day-night sampling. It has also been suggested that planktic larvae may change depths on variable time scales as a means of effecting horizontal movement, by taking advantage of prevailing currents (Garrison, 1999; Miller and Morgan, 2013; Morgan and Fisher, 2010). In addition, a future IBM would benefit from better information on the effects of temperature on embryo hatch dates and larval duration, the prey field during advection, as well as a better understanding of the duration and behavior of megalopae. In analyses detailed elsewhere (Appendix B), addition of one month to the advection period to allow for time spent in the megalopae stage had only limited effect on retention and connectivity trends even given our model assumption that megalopae and zoeae have identical upper water column distributions. Expected vertical movements of megalopae toward the benthos are likely to reduce the advection distance during this stage relative to that during the zoeal stages. Reduced retention in the outer domain during the 1980s was the most notable change observed when adding the extra 30 d of advection (Appendix B).

Although improved future models informed with more and better information are desirable, we propose that our current results are already of value to both managers and fishery stakeholders. Evidence of possible subunits within the EBS Tanner crab metapopulation supports consideration of a spatially explicit stock assessment model with area-specific measures of stock productivity, taking into account estimated larval retention and connectivity patterns. Reductions in uncertainty about stock biomass and productivity parameters would foster better informed management decisions, thus enhancing sustainability of fisheries and reducing the risk of overfishing and the associated costs of resultant fishery closures.

Our findings are supportive of the current ADF&G practice of managing the EBS Tanner crab stock as two sub-stocks east and west of 166° W longitude, rather than as a single stock (Fitch *et al.*, 2012). ADF&G allocates separate catch quotas in each area based on the distribution of exploitable biomass between the two areas. Moreover, if the biomass within one area is below a predefined threshold, no fishing is allowed in that area as has been the case recently in Bristol Bay. This approach contrasts with the Federal fishery management plan under which Tanner crabs are assessed and managed as one unit stock throughout the EBS. The extremely limited advection of floats eastward across the 166° W line suggests it may be inappropriate to pool spawners and recruits from the regions subdivided by this line, as has been common practice in stock-recruit modeling for this species (Zheng and Kruse, 1998, 2003), particularly when examining recruitment in the eastern subdistrict. Development of alternative, more complex, stock-recruit models would need to take into account the asymmetrical and variable retention and connectivity patterns that we have elucidated.

Nevertheless, we have not analyzed our results to determine whether the 166° W line is in the optimal location, nor have we sought to determine whether some smaller subdivisions may be more appropriate. Given the suggested importance of retention to local recruitment dynamics, particularly during years of low abundance, it would appear that the Bristol Bay segment of the EBS Tanner crab metapopulation has limited capacity to recover from its current low abundance via advection of larvae from the Pribilof region, as is also the case of the southernmost portions of the snow crab metapopulation (Parada *et al.*, 2010). This conclusion is consistent with recent observations that the Bristol Bay population segment of Tanner crab has not recovered from the early 1990s collapse, in contrast to those on the middle/outer shelf that have recovered sufficiently to allow recent limited fishing. Thus, Tanner crabs in the Bristol Bay area warrant continued special conservation actions, such as fishery closures while biomass remains below an area-specific fishery threshold.

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Chapter 3:

A Spatially-Explicit Analysis of Proposed Recruitment Mechanisms for Eastern Bering Sea Tanner Crabs[1]

Abstract

Influences of biophysical conditions on survival of zoeal and early benthic stages of eastern Bering Sea Tanner crabs, *Chionoecetes bairdi*, were investigated using the Regional Ocean Modeling System to simulate larval Tanner crab advection patterns from 1978 to 2004. Factors investigated for their potential influence on recruitment of age-3 juvenile crab stemmed from *a priori* hypotheses, and included predation by Pacific cod *(Gadus macrocephalus)*, yellowfin sole *(Limanda aspera)*, and flathead sole *(Hippoglossoides elassodon)*, near-bottom and sea surface temperature, surficial sediments, and cannibalism by 30-50 mm carapace width juvenile or 70-89 mm carapace width subadult male Tanner crabs. We calculated the annual percentages of estimated endpoint locations with conditions meeting hypothesized environmental thresholds for each factor. These percentages were compared against the age-3 yr recruitment index using correlation methods. Visual analysis indicates periods when biophysical conditions at the endpoints may have favored recruitment during the early 1980s, mid-1990s and early 2000s. Our simplest model scenarios performed best; retention in the survey area and settlement in near-bottom temperatures >1° C together explained about 37% of the variability in crab recruitment over 1978-2008. Sea surface temperature, flathead sole CPUE and densities of juvenile crabs were also statistically related to crab recruitment.

[1] Richar, J.I., Kruse, G.H., Curchitser, E., and Hermann, A.J. 2014. A Spatially-Explicit Analysis of Proposed Recruitment Mechanisms for Eastern Bering Sea Tanner Crabs. Prepared for submission to Fisheries Oceanography.

However, our model scenarios with multiple variables performed poorly in explaining juvenile crab recruitment variability. Future field research is needed to better understand behaviors of zoeae and megalopae, as well as functional relationships between survival of newly settled crabs and benthic biophysical conditions.

Introduction

The eastern Bering Sea (EBS) population of Tanner crabs, *Chionoecetes bairdi*, exhibits large variability in survival to maturity and subsequent recruitment to the legal adult male component of the population. Numerous mechanisms have been proposed to influence survival of early life stage Tanner crab based on retrospective analyses of recruitment and ecological variables (Rosenkranz *et al.,* 1998, 2001; Tyler and Kruse, 1997). Follow-up studies with updated datasets (Richar and Kruse, unpublished; Zheng and Kruse, 2006) offered limited support for some previous findings and contradicted others. In this study, we examined a suite of proposed recruitment mechanisms through a spatially explicit approach combining a hydrodynamic simulation model and a geographical information system (GIS).

Tanner crab recruitment variability has been hypothesized to result from mortality during the zoeal and juvenile life stages and a suite of potential mechanisms has been proposed (Tyler and Kruse, 1997); a subset of these were examined by Rosenkranz *et al.* (1998, 2001). Near-bottom temperature (NBT) and northeasterly winds were statistically related to adult Tanner crab abundance at biologically reasonable lags. Warm bottom temperatures were proposed to favor more rapid adult female gonadogenesis and embryonic development, reducing egg predation and losses to disease, whereas northeasterly winds during the pelagic larval stage were suggested to favor advection of larvae to offshore nursery areas predominated

by fine-grained sediments, believed to be preferred by juvenile crabs (Dionne *et al.*, 2003; Paul, 1982). However, a subsequent study with updated wind data found a much weaker correlation to recruitment (Zheng and Kruse, 2006) than did Rosenkranz *et al.* (1998, 2001).

An analysis of groundfish stomach contents concluded that juvenile Pacific cod (*Gadus macrocephalus*) may remove >90% of a given Tanner crab year class, perhaps exerting significant control of crab recruitment (Livingston, 1989). Subsequent stomach content analyses have continued to indicate heavy cod consumption of Tanner crabs (Lang *et al.*, 2003, 2005; Livingston *et al.*, 1993). Despite this empirical evidence, retrospective analyses of Tanner crab recruitment and Pacific cod abundance or biomass failed to detect a negative relationship between cod and crab recruitment in the EBS as would be expected if crabs were under top-down control by cod (Richar and Kruse, unpublished; Rosenkranz, 1998; Zheng and Kruse, 2006). Rather, these studies suggested either no relationship or a positive relationship among the two species. Stomach contents for other groundfish, particularly yellowfin sole (*Limanda aspera*) and flathead sole (*Hippoglossoides elassodon*), indicate that they may also feed heavily on Tanner crabs, in at least some years (Lang *et al.*, 2003, 2005; Livingston *et al.*, 1993, Pacunski *et al.*, 1998). Recent statistical analyses suggest that flathead sole has a negative effect at high densities (Richar and Kruse, unpublished), while providing no evidence for a significant predatory effect by yellowfin sole on Tanner crab recruitment.

Stock-recruit relationships might arise in Tanner crabs through processes including cannibalism (Jewett and Feder, 1983; Sainte-Marie and Lafrance, 2002), disease (Siddeek *et al.*, 2010) and competition for limited resources, such as prey (Paul *et al.*, 1979). If so, then settlement of megalopae in regions with high densities of older crabs may lead to increased

mortality. Zheng and Kruse (1998, 2003) examined male Tanner crab recruitment to legal size as a function of estimated spawner biomass at lags of 7-11 yr, finding weak evidence for a Ricker stock-recruit relationship after incorporating autocorrelation. Richar and Kruse (unpublished) similarly employed a Ricker stock-recruit model with autocorrelation and found strongly negative density-dependent stock-recruit relationships at lags of 2, 3 and 4 yr in three study groups representing two sub-populations east and west of 166° W, in addition to a group representing the full EBS Tanner crab population.

The spatial scales of the retrospective analyses of Tanner crab recruitment conducted to date may not be appropriate for the spatial scale of the hypothesized mechanism. For instance, if the geographic distributions of cod and crabs overlap to varying degrees depending on interannual variability in bottom temperature (Ciannelli and Bailey, 2005), it would be inappropriate to examine potential statistical relationships between cod and crabs based on abundance estimates for the entire EBS continental shelf. The same may apply to variable overlap in spatial distributions of cannibalistic older crab and settling young-of-the-year crabs, at least partly due to interannual variability in larval advection.

Recent advances in computer technology and a better understanding of marine physical processes have facilitated the development of more complex simulation models better able to describe natural processes. As an example, hydrodynamic simulation models, such as the Regional Ocean Modeling System for the Northeast Pacific (ROMS NEP), have been used to study advection patterns for marine fish and invertebrate larvae, providing valuable insights into recruitment dynamics (Hermann *et al.*, 1996; Hinckley *et al.*, 2001; Parada *et al.*, 2010; Stockhausen and Hermann, 2007). In addition, GIS software, incorporating significant

advanced graphical and geostatistical functionality, have greatly simplified the task of studying spatial processes, including ecological conditions, over space and time. Consequently, GIS is a powerful tool for the analysis of biological and ecological data from the aquatic/marine environment, and has been widely applied in recent decades (Bjørge *et al.*, 2002; Guinet *et al.*, 2001; Isaak and Hubert, 1997; Keleher and Rahel, 1996; Nielsen *et al.*, 2007; Stanbury and Starr, 1999). Collectively, these spatial tools offer new means to examine the roles of biophysical factors on Tanner crab recruitment in the EBS.

Here we use an exploratory method to compare spatially explicit transport patterns from a hydrodynamic simulation model against a juvenile Tanner crab abundance index. We test the following hypotheses:

H_1: Survival of juvenile Tanner crabs is positively affected by settling in fine-sediment grain habitats in which they can bury.

H_2: Survival of juvenile Tanner crabs is adversely affected by settling in regions with high densities of cannibalistic 30-50 mm CW juvenile crabs and/or 70-89 mm carapace width (CW) subadult crabs**.**

H_3: Survival of juvenile Tanner crabs is adversely affected by post-settlement exposure to cold NBT (<2°C) associated with the cold pool.

H_4: Survival of juvenile Tanner crabs is adversely affected by increased predation by Pacific cod, flathead sole and yellowfin sole in years when fish distributions overlap those of settling crabs.

H_5: Survival of zoeal stage Tanner crabs is positively affected by warmer sea surface temperatures (SSTs) during the planktic zoeal stages.

H_6: Retention of larvae within the EBS region over the continental shelf is a significant determinant of early life stage survival and recruitment to older age classes.

Methods

Tanner Crab Density and Abundance Estimates

We estimated crab abundance by traditional area-swept methods, as data from a length-based stock assessment model under development for the EBS Tanner crab stock was not yet available (Rugolo and Turnock, 2011). Tanner crab data from annual bottom trawl surveys of the EBS continental shelf conducted during June and July over 1978-2008 were obtained from the National Marine Fisheries Service, Alaska Fisheries Science Center (NMFS AFSC). While the number of stations sampled varied annually during the first decade of sampling, 376 survey stations have been consistently sampled since 1988. A 0.5-hr tow is made near the center of each 20 x 20 nmi^2 (37 x 37 km^2) square on a systematic sampling grid. Since 1982, the standard sampling gear has been a 83-112 Eastern otter trawl using an 83 ft (25.m) head rope and a 112 ft (34.1 m) footrope (Rugolo and Turnock, 2011).

We considered three classes of Tanner crabs: (1) juveniles, (2) males 70-89 mm CW and (3) reproductively active females. For our purposes, we defined juvenile crabs as those of either sex of size 30-50 mm CW. Crabs smaller than 30 mm CW are not effectively sampled by the NMFS bottom trawl, while crabs larger than 50 mm CW likely represent a mix of multiple-aged cohorts owing to growth variability. Reproductively active female Tanner crabs were defined as those of shell condition 3 (SC3, old shell) and shell condition 4 (SC4, very old shell) (see Jadamec *et al.*, 1999 for descriptions of shell conditions), summed by station. We did not include SC5 female crabs and excluded most SC2 crabs from our estimates. Primiparous or

SC2 female crabs were primarily excluded because they have an extended brooding period (Swiney, 2008). Consequently, SC2 crabs sampled in year *t* should hatch their eggs in year *t+1*, and thus not contribute to the age-3 juveniles in year *t+3* used as the response variable in our analyses. Instead they would be counted as SC3 crabs when encountered by the survey the following year. An exception was made for SC2 females bearing eyed embryos, as this is an indication of advanced gestation associated with mating in year *t*-1 (Dr. Jie Zheng, Alaska Department of Fish and Game, pers. comm.). Shell condition 5 crabs were ignored due to comparatively high rates of barrenness, lower fecundity and low abundance (Joel Webb, Alaska Department of Fish and Game, pers. comm.).

To prevent bias in float apportionment due to differences in reproductive output and spatial distributions between SC3 and SC4 females, the abundance estimates of SC4 female at each station were weighted relative to corresponding SC3 estimates to account for reduced fecundity and egg bearing rates (Joel Webb, Alaska Department of Fish and Game, pers. comm.) using eq. (3.1):

$$SC4_w = \left(\frac{SC4_f}{SC3_f}\right) * \left(\frac{SC4_{eb}}{SC3_{eb}}\right), \qquad \text{[eq. 3.1]}$$

where $SC4_w$ = the weight function by which shell SC4 female density estimates were multiplied to standardize their potential reproductive potential relative to SC3 females, $SC3_f$ = shell condition 3 female fecundity, $SC4_f$ = shell condition 4 female fecundity, $SC3_{eb}$ = shell condition 3 egg bearing rate and $SC4_{eb}$ = shell condition 4 egg bearing rate. For males 70-89 mm CW and reproductive females, estimated density $\widehat{D}$ at station *j* in year *i* was calculated as:

$$\widehat{D}_{ij} = \frac{\sum_k S_{ijk} * N_{ijk}}{A_{ij}}, \qquad \text{[eq. 3.2]}$$

where N_{ijk} = number of crabs in class k sampled at station j in year i, S_{ijk} = the estimated sampling factor for crabs in class k at station j in year i, and A_{ij} = the estimated area swept at station j in year i in km^2. The sampling factor accounts for subsampling of large hauls, and expands the number of crabs sampled for biological information and listed in the database to the number actually captured by the trawl tow at that station. For juvenile crab density estimates, we used eq. (3.2), modified to account for reduced catchability of the smaller juveniles (q = 0.30, Somerton and Otto, 1999) relative to adults. To generate a juvenile recruitment index, we first calculated mean density per station in year i ($\overline{D}_i$):

$$\overline{D}_i = \frac{\sum_j \frac{\hat{D}_{ij}}{q}}{n_i}, \qquad \text{[eq. 3.3]}$$

where n_i = number of stations sampled in year i. We then calculated annual area-swept abundance estimates for a given year ($\overline{N}_i$):

$$N_i = \overline{D}_i * n_i * a, \qquad \text{[eq. 3.4]}$$

where N_i is the area-swept abundance estimate for year i and a is the area of each survey grid square. Next, we calculated a natural log-abundance recruitment anomaly time series based on this recruitment index, which was standardized by the standard deviation of the natural log-abundance time series:

$$R_i = \frac{(\ln(N_i) - \overline{\ln(N)})}{s_{\ln(N)}}, \qquad \text{[eq. 3.5]}$$

where R_i = the annual standardized abundance anomaly estimate and $s_{ln(N)}$ = the standard deviation of the natural log of juvenile crab abundance. Hereafter, we refer to this as the

juvenile abundance residual series. This series demonstrates a cyclical pattern similar to that observed in stock-recruit model residuals (Fig. 3.1, Richar and Kruse, unpublished), with statistically significant positive and negative autocorrelation occurring at lags of 1 and 7 yr, respectively (Fig. 3.2).

Regional Ocean Modeling System (ROMS)

We employed the ROMS Northeast Pacific model-5 (NEP5), developed for the Northeast Pacific Global Ocean Ecosystem Dynamics (GLOBEC) research program (Curchitser *et al.*, 2005). The NEP5 was a free-surface hydrostatic primitive equation ocean circulation model run over a 5-km resolution grid and used data on environmental forcing variables obtained from the Common Ocean-ice Reference Experiments (CORE, Large and Yeager, 2008) to simulate circulation patterns. These included observations of both wind direction and magnitude measured at 6-hr intervals, atmospheric temperatures, sea level pressure, specific humidity, incident solar radiation and monthly precipitation levels (Danielson *et al.*, 2011). River discharge is incorporated as a spatially dependent, constant surface freshwater flux that preserves regional fresh water budgets, albeit while introducing inaccuracies into the local salinity calculations (Danielson *et al.*, 2011). In the horizontal plane, model equations are discretized across a staggered Arakawa C-grid using boundary-fitted orthogonal curvilinear coordinates (Danielson *et al.*, 2011). Vertically, we employed 10 model layers to capture variability in water column features. Within these layers, model equations are discretized over bathymetric features by means of a terrain-following coordinate system, allowing model resolution to be increased as necessary near comparatively complex boundary layers at the surface and bottom of the water column (Danielson *et al.*, 2011). Finally, tracer

advection is accomplished using weakly dissipative algorithms wherein sharp gradients in oceanographic properties, such as fronts, are not smeared out in the process of advection across model grid points (Danielson *et al.,* 2011).

Critical model parameters for Tanner crab zoeae, including timing and pattern of release, float depth distributions and advection duration were derived from field observations (Incze *et al.*, 1987). In the EBS, larval release begins in late April, peaks in mid May, and then tapers off, ending in June (Incze *et al.*, 1987). Approximately 80% of zoeae are found within the first 20 m of the water column, with > 90% in the upper 40 m (Incze *et al.*, 1987). There is no evidence of diel migration; depth-specific sampling indicated similar larval depth distributions during day and night (Incze *et al.*, 1987). Following field observations (Incze *et al.*, 1987), we modeled a larval period of two months, divided equally between two zoeal stages. We ignored advection during the megalopae stage, as little is known about behavior and duration of this stage. Similarly, in a ROMS modeling study of congener snow crab *(Chionoecetes opilio)* in the EBS, Parada *et al.* (2010) assumed that larval "settlement" occurs at the start of the megalopa stage, as megalopae were presumed to be demersal or hyperbenthic.

Float starting locations were derived from density distributions of reproductive female crabs from NMFS trawl survey data (eq. 3.2), which were assumed to be representative of female distributions at the time of spawning (1-4 mo previously); numbers of floats per station were proportional to estimated female density. Female surface density (crabs/ km^2) was divided by 5 to conserve computation time and converted to an integer to determine the number of floats released at that station. Model floats were released near the center of each NMFS survey station. Floats were released uniformly over a period of 10 d for each station. Initial release

ranged over April 17 □ 27, with final release ranging from May 25th to June 6th (Table 3.1). Longer release periods were employed during years with higher female abundances to capture variability in release timing due to environmental and physiological variability that may be more pronounced during years of high female abundances. Typically, 5,000-10,000 floats were released annually, with a maximum of 60,232 (1982) and a minimum of 881 (1986). To mimic the observed distribution of larvae (Incze *et al.*, 1987), floats were released across water column depth ranges of +/- 2 m, centered at approximately 10 m (~75% of floats), 30 m (~15% of floats), and 50 m (~10% of floats).

Due to lack of behavioral information, we assumed that drifting larvae maintained their vertical position in the water column. Therefore released floats were constrained to remain at a constant pressure. Model estimated float locations after 60 d, corresponding to the approximate temporal duration of the two zoeal stages (Incze *et al.,* 1982), were considered to represent the model estimated endpoint locations. Simulations were conducted for each year during 1978-2004.

Recruitment Factor Mapping

Ordinary kriging procedures in ESRI ArcGIS 9.3 Spatial Analyst (ESRI, 2009) were used to interpolate spatial distributional maps of the hypothesized recruitment factors. Maps were sampled at endpoint locations after 60-d using the Spatial Analyst Extract-to-Point tool to determine the value of each factor at each endpoint. In addition to 70-89 mm CW subadult male and 30-50 mm CW juvenile crab densities, factors included NBT and groundfish catch-per-unit-effort (CPUE) from the annual trawl survey. Summer NBT is measured by temperature loggers attached to survey trawl gear; data were extracted from the EBS trawl

survey database for 1978-2008 (Dr. Robert Foy, NOAA AFSC, pers. comm.). Survey CPUE (in kg/ha per station) of Pacific cod, yellowfin sole and flathead sole over 1982-2008 were obtained from the survey database (http://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm). Due to the timing of megalopae settlement and groundfish seasonal migrations (Shimada and Kimura, 1994; Wilderbuer *et al.*, 1992), we assumed that most groundfish predation on young crabs occurred 1 and 2 yr post-settlement. Use of the CPUE time series limited our considerations of groundfish predation to the period beginning with the 1981 pseudocohort, as the CPUE data began in 1982, and the assumption that predation did not become significant until the year after release and settling.

Surficial sediment distributions from the Alaska Peninsula north to St. Lawrence Island and from the western Alaska coastline west to the shelf break were obtained from Naidu (1988). Paper maps were scanned and the digital images were georeferenced in ArcGIS 9.3. A polygon shapefile was created to represent sediment distributions, which was converted to a raster for ease of use. Nine sediment classes and their assigned numerical value are: (1) gravel, (2) muddy gravel, (3) gravelly sand, (4) gravelly muddy sand, (5) sand, (6) muddy sand, (7) gravelly muddy sand, (8) sandy mud, and (9) mud.

The ROMS tracks mean daily SST encountered by each float during advection. These daily values were averaged over the 60-d advection period to obtain mean SSTs for each float.

Multivariable Threshold Gauntlet Models

We examined trends in the percentages of model endpoints meeting a set of pre-specified biophysical habitat conditions. Different combinations of these conditions, each

represented by a different scenario, reflect the different *a priori* hypotheses about habitat suitability. These hypotheses were then tested by correlating the annual percentages of model endpoints in suitable habitat meeting specified thresholds with trends in juvenile Tanner crab recruitment. For instance, our first hypothesis was that crab survival is enhanced by settling in fine-sediment grain habitats. However, we did not know how fine the sediment should be. As a first step, we plotted the sample means for each factor averaged across all model endpoints within the survey area, by year, to assess long-term trends in the factors themselves, and to determine potential thresholds of each factor for survival of settling crabs. Although it would be convenient if a single factor explained the majority of recruitment variability, early life stage survival in a complex system such as the EBS is likely to be determined by exposure to multiple mortality factors acting synergistically over varying time scales. Consequently, we also modeled scenarios in which the biophysical factors of interest were examined simultaneously by assigning values based on initial exploratory plots (30-50 mm CW and 70-89 mm CW crab densities, and CPUE for Pacific cod, flathead and yellowfin sole), reports of apparent crab preferenda/tolerances (NBT (Paul and Paul, 2001) and sediment class (Nielsen *et al*., 2007; Rosenkranz, 1998), or proxies for assumed Tanner crab tolerances (SST, Incze *et al.*, 1987; Rosenkranz, 1998; Smith and Vidal, 1984). Threshold values associated with improved survival were either minima or maxima, depending on the factor in question:

$$n_y = n(F_1 < T_1, F_2 < T_2 \ldots\ldots and\ T_x > F_x), \qquad \text{[eq. 3.6]}$$

where n_y = the number n of endpoints in year y meeting the criteria as specified by each threshold, F_1 and F_2 are values of two factors below their hypothesized corresponding thresholds T_1 and T_2 that favor survival (e.g. sole or cod CPUE), and F_x is a factor for which

values above threshold T_x favors survival (e.g. NBT, Table 3.2). The annual percentages of endpoints, P_y, meeting all hypothesized threshold conditions were then calculated as:

$$P_y = \frac{n_y}{N_y} * 100, \qquad \text{[eq. 3.7]}$$

where N_y = the total number of floats released in year y. Annual percentages for each threshold scenario were plotted as time series for comparison among scenarios and with the crab recruitment series.

To begin, we examined retention alone. To establish baselines, we then added each of the other factors of interest singly and at one lag, with initial threshold values determined using the aforementioned methodologies. We then expanded upon these baselines by adding each of the lags investigated for that factor to subsequent scenarios, culminating in a scenario with all lags investigated for each factor of interest. Threshold values were then varied within biologically reasonable bounds to allow for tolerances/preferenda differing from our beginning assumptions. For groundfish CPUE and crab densities, we also created scenarios focusing on all agents for a particular mechanism (predation or cannibalism), considering CPUE for all groundfish together, and densities of both crab categories together, while excluding all other factors. In our reporting, for simplicity, we classify these mechanism-based scenarios and those focusing on a single factor as being our "simple" or "single-factor" analyses. Beginning with scenario 170, all factors were included. For analyses following scenario 170, one factor was chosen and its threshold value was varied incrementally within reasonable bounds while all other factors remained fixed. For each level considered for that given factor, a second factor was chosen and its threshold(s) varied while all other factors remained fixed, and so on. In our

reporting, we classify these as being our "multifactor" analyses. We did not examine all possible combinations, and terminated analyses after scenario 686 to maintain a manageable workload, and because it had become apparent that further multifactor scenarios would be unlikely to improve upon the initial single factor/mechanism analyses. For NBT, thresholds were investigated as both upper and lower thresholds, due to the potential for warmer temperature to increase predation by groundfish. Also, in one subset of multifactor analyses, NBT thresholds were incrementally increased with lag post-settlement to allow for possible decreased tolerance/preference for cold temperatures with ontogeny, as observed in *opilio* crabs (Dionne *et al.*, 2003).

Because the kriging procedures calculated estimates for NBT, groundfish CPUE and crab density beyond the spatial extent of the actual survey data, these spatially extrapolated values were not considered reliable. Consequently, only floats whose modeled endpoints were within the Tanner crab survey region were included in the analysis. Exclusion of model extrapolated values outside the survey area also maintains validity of spatial comparisons between the juvenile crab index and sampled ecological data.

Time series of the proportion of endpoints meeting a given set of hypothesized threshold conditions were visually assessed for trends approximating those of recruitment to the juvenile and adult crab populations (e.g. Fig. 3.1). Strength of agreement between patterns in these time series and the juvenile Tanner crab residual series was determined by calculating Pearson’s correlation coefficient for each pairing using both basic correlation methodologies and, for comparison, methods that account for autocorrelation (Pyper and Peterman, 1998). For the latter, modified degrees of freedom were calculated as:

$$\frac{1}{N*} = \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{\infty}\frac{N-j}{N}\rho XX(j)\rho YY(j), \quad \text{[eq. 3.8]}$$

where N^* is the effective degrees of freedom, N is the sample size (24) and ρXX and ρYY are the autocorrelations of time series X and Y at lag j. Using the effective degrees of freedom a modified standard critical value for the correlation between the datasets is then calculated as:

$$r^* = \sqrt{t^2_{\alpha,\, N^*-2}\left(t^2_{\alpha,N^*-2} + N^* - 2\right)}, \quad \text{[eq. 3.9]}$$

where r^* is the standard critical value adjusted for autocorrelation and N^* is the modified degrees of freedom as in eq. (3.8) with 2 degrees of freedom subtracted. Two tailed *t*-tests were used in all analyses to reduce the likelihood of detecting spurious correlations and because we were not always sure of the sign of the effect.

Herein, due to the number of scenarios modeled (n = 686) we focus our reporting efforts on those with either statistically significant (α = 0.05) correlation values:

$$|r| > \frac{2}{\sqrt{N}}, \quad \text{[eq. 3.10]}$$

or ~ 0.4.

Results

Results were variable depending on the factor in question, choice of lag, and threshold(s) employed. In most scenarios, several periods were observed when, under the assumptions of the scenario, conditions may have favored crab survival. In general, simpler (1-3 factor) scenarios offered superior performance, measured on the basis of correlation strength, in comparison to more complex scenarios incorporating all or most of the factors of interest. Of the factors investigated, NBT >1.0° C had the strongest correlation with recruitment (r = 0.61), while the strongest correlations for the remaining factors were often observed when these were

considered in concert with NBT. Methods to account for strong autocorrelation in the juvenile crab recruitment series greatly reduced the number of statistically significant correlations, with NBT being a factor in all but one of the remaining scenarios.

Mean annual retention within the region sampled by the AFSC trawl survey, was consistently high during most of the study period, with the lowest retention rates (~73%) in the early 1980s (Fig. 3.3). Ecological conditions at model estimated endpoints were variable in both space and time for each factor considered, due to interannual differences in float transport and changes in the factors themselves, though some trends were observed, particularly through time. For instance, Pacific cod CPUE at the endpoints peaked during the early 1980s, but began to decline after 1985 (Fig. 3.4a). During the 1990s and early 2000s, average Pacific cod CPUE remained under 20 kg/ha, except during 1993-1994, when a brief peak, with mean CPUE of 25-30 kg/ha, was observed. Yellowfin sole CPUE was particularly variable; during the early 1980s CPUE averaged ~30 kg/ha, with a record peak of ~120 kg/ha in 1987, then declined rapidly, maintaining an average of ~50 kg/ha through most of the 1990s. In the early 2000s it declined further, averaging <25 kg/ha (Fig. 3.4b). Trends in flathead sole CPUE showed the opposite trend, gradually increasing from <10 kg/ha during the early 1980s to ~25 kg/ha in the early 2000s (Fig. 3.4c).

Temporal trends in the remaining ecological factors were also variable, with some notable features. Mean sediment class at the endpoints had no discernible trend, though the mean varied between 6 (muddy sand) and 8 (sandy mud) over the study period due to differences in transport vectors, and thus estimated endpoint locations (Fig. 3.4d). For NBT, at all three lags investigated, warmest conditions at endpoints were in the early 1980s and early

2000s; mean NBT at the endpoints from the late 1980s through late 1990s was typically <3.0º C and often < 2.0º C (Fig. 3.5a). Mean SST along the float tracks shows a similar trend with warmest temperatures in the early 1980s and 2000s and generally cooler conditions during the late 1980s and 1990s (Fig. 3.5b). Mean densities of large juvenile male crabs at the endpoints were typically well under 800 crabs/km^2, except during the late 1980s population spike, and in the early 2000s, when mean densities ranged between 1000-1200 crabs/km^2, with most of the 1990s being typified by densities <400 crabs/km^2 (Fig. 3.5c). Finally, mean densities of small juvenile crabs were extremely variable, ranging from <200 crabs/km^2 during the mid-1990s to >5000 crabs/km^2 during the early 2000s. During the late 1980s population boom, small juvenile densities ranged between 1000 and 2000 crabs/km^2 (Fig. 3.5d).

Gauntlet analyses suggested at least two periods when, with all factors considered together, conditions may have favored early juvenile survival. These periods were found to occur in the majority of scenarios and roughly corresponded to recruitment patterns at biologically reasonable time lags. Length of these periods and the percentage of endpoints meeting the specified thresholds varied with the threshold value settings. A third lesser period was observed under only certain settings.

The first of these periods occurred during the early to mid 1980s (e.g. Fig. 3.6). During this interval typically 3-14% of endpoint locations experienced conditions within the hypothesized thresholds, dependent on the scenario, with an extreme of ~25%. The percentages of floats meeting thresholds annually, and the number of years for which this occurred were highly responsive to Pacific cod, due to relatively high CPUE being observed at model endpoints during the early 1980s (Fig. 3.7). In addition, the percentage of floats meeting

thresholds during this period was also notably affected by NBT thresholds (not shown), and by those for both juvenile crabs and large juvenile crabs (not shown), though to a more limited degree, with the strongest effects for the latter being apparent during the population expansion at the end of that decade.

The second period during which conditions at the endpoints may have favored juvenile survival occurred primarily during the mid-late 1990s, but continued into the early 2000s under certain conditions (Fig. 3.6). During this time, 4-10% of model floats encountered conditions within hypothetical survival thresholds, with a maximum of 20% occurring in several scenarios. In contrast to the earlier period, much lower Pacific cod CPUE was observed at the model endpoints, and a general decline continued through the decade (Fig. 3.7, 3.8). As a consequence, this factor was not an important determinant of habitat suitability during this period. Conversely, flathead sole CPUE at the endpoints increased such that it surpassed Pacific cod CPUE, and became an important criterion for habitat suitability (Fig. 3.7). During the 1980s and the period 1997-1999, cold NBT at the endpoints was an important determinant of the number of endpoints in suitable conditions (2-14%). Due to low population densities, large male juvenile crabs were an insignificant factor on modeled survival throughout the 1990s, requiring very low threshold value settings to have measurable effects.

A third period occurred in the early 2000s (not shown) under certain liberal assumptions regarding the densities of both 30-50 mm CW juvenile and 70-89 mm CW large juvenile male crabs at which cannibalism and other density dependent effects would become an important recruitment factor (>1000 crabs/km^2).

The best results for our correlation analyses were observed in scenarios involving only 1-3 factors. More complex scenarios employing combinations of factors performed comparatively poorly. The percentages of model floats meeting specified thresholds were positively associated with juvenile crab recruitment for the majority of scenarios considered, with 24 positive correlations that were statistically significant at $\alpha = 0.05$ (Table 3.3). In addition, 19 statistically significant correlations were negative and were primarily observed in scenarios involving low densities of juvenile Tanner crabs (Table 3.3). Because of generally high retention over the study period, retention on its own did not demonstrate a statistically significant relationship with the juvenile crab residuals. Inclusion of retention in the baseline scenarios with other factors, for reasons as previously outlined, had limited, generally positive effects on relationship strength, typically increasing correlations by ~0.05-0.1.

Our best performing scenario (144) explained 37.2% of the variance in observed recruitment ($r = 0.61$) and involved a combination of retention within the study area and NBTs >1.0º C during the first 3 yr of life (Table 3.3, Fig. 3.9). Mean modeled sea surface temperature added little descriptive capacity to multifactor scenarios, but gave suggestive results in our simpler scenarios. Threshold values of >3.0º C and >4.0º C for SST had statistically significant correlations ($r = 0.41$ and 0.48 respectively) in basic scenarios combining only retention and SST (Table 3.3). However, results for thresholds of 2.0º C and 5.0º C were insignificant. When considered in concert with both retention and NBT, scenarios with SST thresholds of 3.0º C and 4.0º C resulted in statistically significant correlations, however incorporating SST weakened relationships relative to the retention and NBT-only scenarios, with the relationship progressively weakening as SST thresholds were raised (Table 3.3).

Several flathead sole-based scenarios performed well, with a moderate threshold of <30 kg/ha, giving our best correlation value (r = 0.53) for a scenario not including NBT (Table 3.3). The percentage of floats below a high threshold of 40 kg/ha was more weakly correlated with the juvenile residuals, while a correlation of r = 0.39 was associated with a low threshold of 20 kg/ha, suggestive of a relationship, but not statistically significant.

Low to moderate juvenile (30-50 mm CW) crab densities at the endpoint locations were negatively correlated with recruitment across a range of thresholds (Table 3.3). The strongest correlation (r = -0.50) was observed at a moderate upper threshold value for juvenile crab densities (<1000 crabs/km^2) in both the hatch/settlement year and the following year, with correlations weakening to the point of insignificance at higher thresholds (Table 3.3). For large juvenile (70-89 mm CW) male crabs, scenarios combining retention, NBT > 1.5° C and > 2.0° C and crab density thresholds of <500 crabs/km^2 and <600 crabs/km^2 were significant. In addition, scenarios combining (with thresholds) retention, SST (>3.0º C and >4.0º C) NBT (>1.5º C and >2.0º C) and large juvenile male crabs (>500 crabs/km^2 and >600 crabs/km^2) were statistically related to juvenile crab recruitment trends. However, correlations were lower than those observed in the retention and NBT-only scenarios, indicating that inclusion of SST and large juvenile male crabs was counterproductive.

Pacific cod and yellowfin sole densities and sediment class at endpoints failed to demonstrate a strong relation to juvenile crab recruitment levels, with the only significance for these factors being observed in exploratory scenarios having very high thresholds for all three groundfish species (Table 3.3). The majority of sediment class observations at the estimated endpoint locations were fine-grained mixes of sand/mud or mud.

When adjusting for autocorrelation in the time series, only 5 correlations were statistically significant (Table 3.4). All of the significant relationships included either sea surface temperature or NBT at biologically reasonable thresholds (Table 3.4). Scenario 144, involving retention and NBT >1.0° C, remained the most statistically significant model. As in non-adjusted correlation analyses, while scenarios combining SST and NBT with retention were statistically related to recruitment, relationships were weaker than the scenario with only retention and NBT used as their baseline (Table 3.4).

Discussion

We examined a suite of ecological factors that were hypothesized to regulate recruitment of EBS Tanner crabs by comparing the spatial distributions of these factors against larval endpoint locations estimated by a state-of-the-art ROMS hydrodynamic model. These results were then compared against interannual trends in juvenile crab recruitment to identify likely recruitment mechanisms. Our results indicate periods for enhanced crab post-settlement survival during the early to mid 1980s and mid to late 1990s and possibly in the early 2000s. Our results further offer varying degrees of support for the hypotheses that SST, NBT, flathead sole and larger juvenile crabs are related to juvenile Tanner crab recruitment success.

Of the factors we investigated, NBT had the strongest relationship to juvenile crab survival, explaining up to 37% of crab recruitment variability, with the strongest results obtained using survival threshold values of >1.0-1.5° C. This threshold would exclude most of what is commonly defined as the cold pool (<2.0º C), with only the warmer periphery being suitable for settlement and subsequent habitation by early juvenile stages. Analysis of interannual trends in mean NBT at the endpoints further indicates a mean temperature at the

endpoints at or below 2.0º C for much of the 1990s. The congener snow crab, *Chionoecetes opilio*, is tolerant of conditions found within the cold pool (Webb *et al.*, 2007), and may require cold conditions, particularly during its juvenile stages (Comeau *et al.*, 1998; Parada *et al.*, 2010; Orensanz *et al.*, 2004). Tanner crabs are thought to be less cold tolerant (Rosenkranz, 1998; Rosenkranz *et al.*, 2001; Tyler and Kruse, 1997). NOAA surveys indicate that mature female crabs occur primarily beyond the boundary of the region usually covered by the cold pool. Both legal and sublegal male Tanner crabs show distributions similar to those of mature females (Rugolo and Turnock, 2011). However, survey data indicate that juvenile Tanner crabs occur in the periphery of the region typically covered by the cold pool, particularly in the southern portion of the middle domain, suggesting that they have at least some capacity to tolerate temperatures found along the margins of the cold pool. In the laboratory, juvenile Tanner crab growth was slower at 3.0° C than at 6.0° and 9.0° C treatments, with a mean intermolt period of 154 days observed, versus 78 and 74 days, respectively; yet, no additional mortality occurred at the colder temperature and feeding activity was not reduced (Paul and Paul, 2001). While Tanner crab tolerances to temperatures colder than 3.0° C have not been examined in the laboratory, tolerance of 3.0° C without apparent ill effects suggests at least some capacity to tolerate temperatures below, but close to, this threshold.

Our findings support the hypothesis that warmer SST during the larval phase may benefit early life stage success and subsequent recruitment. The threshold of 3.0º C matches the thermal minima for successful growth and reproduction of *Acartia* spp. and *Pseudocalanus* spp. copepods (Smith and Vidal, 1984), proposed as an important component of the diet of zoeal Tanner crabs (Incze *et al.*, 1987; Rosenkranz, 1998). Statistical relationships at warmer

threshold values may represent beneficial effects of increased temperature on the reproduction and development of these prey of crab larvae. Alternatively, warmer temperatures may increase larval crab growth rates and reduce duration of the larval period, thus reducing vulnerability to predation during this especially vulnerable life stage (Hare and Cowen, 1997). Nevertheless, inclusion of SST in model scenarios with NBT and retention did not improve agreement with observed Tanner crab recruitment trends and, in fact, resulted in slightly lower correlations. At best, this suggests that SST may have limited explanatory power beyond effects indexed by NBT.

Our findings provide limited support for the hypothesis that cannibalism by large (70-89 mm CW) juvenile male crabs controls Tanner crab recruitment. The strongest evidence of cannibalism was associated with scenarios incorporating cannibalism, SST and NBT. However, these correlations were lower than those observed in both baseline NBT-only scenarios and those involving SST and NBT without cannibalism, suggesting that cannibalism did not add explanatory power. When autocorrelation was taken into account, no scenarios including large juvenile crabs were statistically significant. While *Chionoecetes* spp. are known cannibals (Jewett and Feder, 1983; Sainte-Marie and Lafrance, 2002), the most convincing observations of cannibalism were made in fjords and small bays (Sainte-Marie and Lafrance, 2002), confined habitats combining high densities with limited opportunities for evasion. The broad, flat EBS continental shelf affords a far greater habitable area with fewer obstacles to evasion, possibly reducing intercohort interactions sufficiently to limit effects of cannibalism.

We observed a negative relationship between juvenile recruitment and lower densities of 30-50 mm CW juvenile crabs at the endpoint locations, opposite the expectation under the

hypothesis of cannibalism that low densities would be positively related to crab recruitment. This may arise due to autocorrelation present in juvenile crab population trends which was reflected in both our density estimates and the juvenile crab recruitment time series. A less-likely alternative is that high juvenile crab densities may reflect so-called nursery habitats which were not indexed by our other biophysical datasets, with higher juvenile crab densities being found at endpoint locations within these regions.

Our results provide mixed support for the hypothesis of a predatory effect by groundfish. High Pacific cod CPUE was observed at model settlement locations during the early-mid 1980s, consistent with low recruitment in the early 1980s (Fig. 3.1), and also consistent with analyses of stomach contents indicating high predation of juvenile Tanner crabs by cod during these years (Livingston, 1989). However, inclusion of top-down control from Pacific cod did not improve the overall fit, because cod CPUE declined during the 1990s concurrent with the decline in Tanner crab recruitment. Our results are consistent with other retrospective analyses (Richar and Kruse, unpublished; Rosenkranz, 1998), which failed to find evidence of a cod effect on Tanner crab recruitment. Conversely, while flathead sole CPUE at the endpoints was low during the 1980s, it increased during the 1990s, becoming an important factor for modeled crab survival during the 1990s. This is consistent with the geographic expansion of the EBS flathead sole in the 1990s, and may indicate a hand-off in predatory effect on Tanner crabs between these two species; Pacific cod were the major predator during the 1980s, while flathead sole took over this role in the 1990s, as indicated by stomach content analyses (Lang *et al.*, 2003, 2005; Livingston *et al.*, 1993). Unlike Pacific cod, flathead sole

CPUE was statistically related to Tanner crab trends at reasonable thresholds roughly equivalent to the late 1990s mean CPUE.

The only significant correlations for yellowfin sole were found in scenarios incorporating all three groundfish species, with moderate-high thresholds. These results are somewhat surprising, as yellowfin sole CPUEs, while variable, were typically very high relative to both Pacific cod and flathead sole at the estimated endpoint locations. However, while dietary analyses show that yellowfin sole feed on juvenile crabs, prevalence of crabs in stomach contents is highly variable, and may not support an interannually consistent predatory relationship (Lang *et al.*, 2003, 2005; Livingston *et al.*, 1993).

There may be interplay between the potential effects of cold NBT and predation on crab recruitment, which should be considered when interpreting results of our analyses of these factors. For instance, both Pacific cod and flathead sole appear to avoid the cold pool, which may limit their penetration of the middle domain during summers following severe winters (Ciannelli and Bailey, 2005; Rooper *et al.*, 2005). In particular, flathead sole appear to have a narrow thermal preference, seeming to prefer a temperature range of 2.0° to 4.0° C, likely due to an apparent high Q_{10} (Q_{10} = 6.3, Mineva, 1964; Paul *et al.*, 1995; Rooper *et al.*, 2005). Considering the high percentage of model endpoints we observed within the cold pool (<2.0° C), such avoidance behavior suggests that settling at least within the periphery of the cold pool may have the potential to reduce predation on juvenile Tanner crabs, possibly offsetting deleterious growth effects from cold temperature exposure. This may offer an explanation for the difficulty in finding an unambiguous relation between Tanner crab recruitment and both groundfish and NBT. Namely, cold pool conditions colder than those observed in the

laboratory (Paul and Paul 2001), but above some absolute survival threshold, may adversely affect growth and cause some juvenile mortality, while at the same time exclude predators such that these effects are offset. Conversely, warmer temperatures would favor growth in the juvenile crabs and reduced mortality due to exposure, but may also increase mortality due to increased predation.

All three groundfish species display large-scale seasonal migratory behavior within the EBS region, complicating any interpretation of these findings. Both Pacific cod and yellowfin sole overwinter in the deep, warmer offshore waters of the outer domain, then move onshore in spring, with the movement of Pacific cod in particular being influenced by the extent of the cold pool (Ciannelli and Bailey, 2005; Nichol, 1998; Shimada and Kimura, 1994; Wilderbuer *et al.,* 1992). While flathead sole migratory patterns are not as well documented, this species demonstrates significant interannual variability in distributions apparently linked to the extent of the cold pool (Spencer, 2008). Unfortunately, due to data limitations it is not possible to track interseasonal changes in groundfish distributions at this time.

Our results do not support the hypothesis that sediment class at settlement comprises a recruitment mechanism for eastern Bering Sea Tanner crabs. We hypothesized that megalopae and juvenile crabs would likely prefer muddy sediment due to the preponderance of very small sediment grains for burial to avoid predators. These sediments, however, have a fairly wide distribution within the eastern Bering Sea, and examining sediment class separately from all other factors reveals that, while a large number of endpoint locations were indicated to have sediments with larger grain size (i.e. sand and gravel), fine grain sediments dominate. Likewise, when considered alone, the percentage of floats retained in the Tanner crab survey area was

insufficient to explain recruitment variability. Sluggish, predominately along-shelf currents appear to limit the capacity for larvae to be advected beyond the bounds of the trawl survey area to a much greater extent than we had hypothesized.

We would be remiss if we did not point out that, given the number of comparisons made (n = 686) and the significance level used (α = 0.05), one would expect 34 significant correlations to be found due to chance alone. Consequently, there is a high likelihood of many spurious correlations. While we attempted to reduce the chances of spurious correlations by pre-selecting variables for inclusion based on laboratory, field and retrospective analyses, uncertainties about functional relationships (e.g. thresholds) led us to investigate multiple scenarios for the different factors, either singly or in combination with other factors. We also recognize that cross-correlations among variables may lead to errant conclusions about cause and effect. On the other hand, many hypotheses about factors affecting Tanner crab recruitment exist (e.g. Tyler and Kruse, 1997), and we have investigated the consistency of these mechanisms with field observations in the context of a realistic oceanographic model.

Our results are predicated on the validity of the NEP5 model and its applicability to the EBS continental shelf region. Danielson *et al.* (2011) demonstrated NEP5 to effectively recreate the hydrography of the EBS region, though with some caveats. It has been observed that NEP5 slightly overestimates mean current velocity relative to corresponding field observations across much of the EBS shelf, though differences between observed and simulated velocities were generally within the 95% confidence intervals for observed current estimates (Danielson *et al.*, 2011). Performance within the middle domain is unknown: comparisons of modeled and observed currents within the middle domain were not considered to be reliable

due to the highly variable nature of flow within that region, and validation has not been attempted (Danielson *et al.*, 2011).

Model resolution in both the horizontal and vertical axes is critical both to capture small scale features within the current system that may influence float trajectories, and to allow for complex shorelines and seafloor features that may modify currents. The EBS shelf maintains a gradual low relief slope from the western Alaska coast to the shelf break: the only significant deviations from this are primordial shorelines approximately marking the 50 and 100 m isobaths, and the Pribilof and St. Matthew Islands. Further, current systems advected floats away from the northern Alaska Peninsula, which comprised the only complex shoreline within the study region, limiting the potential for shoreline interactions to influence advection. Moreover, the hydrography of the EBS region is comparatively low energy across much of its extent relative to many other regions of the global sea, with only limited mean long term flows (Coachman, 1986). As such, for our purposes, the resolution of NEP5 (horizontal: 10 km x10 km, vertical: 10 layers) was judged adequate.

Due to the lack of empirical information on Tanner crab ecological tolerances, we were forced to use hypothetical values for our thresholds. We acknowledge that this constitutes a notable concern with our methods, and consider this study and its results to be exploratory. Alternative methodologies exist, but present problems of their own. Distribution-based analyses (Perry and Smith, 1994) allow visual comparison of single year, single factor data distributions and relatively straightforward statistical determination of similarity/dissimilarity. Analysis, interpretation and summarization may, however, be cumbersome when the number of comparisons being made is high, requiring use of subsets of data that may not be

representative. In addition, depending on sample size, statistical tests may be excessively sensitive to even small differences in the distributions, leading to misleading conclusions. Finally, the single factor nature of these analyses does not lend itself to approaching complex ecological questions that may be affected by multiple factors (Kruse and Tyler, 1989; Worm and Meyers, 2003), which may lead to at best ambiguous results (e.g. Appendix C).

Owing to the limited state of current knowledge regarding Tanner crab early life history, we had to employ a non-individual based model for larval advection that was relatively simplistic in comparison to some others (Parada *et al.*, 2010). Before an individual-based model can be reasonably attempted for Tanner crabs, a number of data limitations must be addressed. Of particular concern is the potential for vertical movement within the water column by zoeae either as part of a diurnal migration, or as directed movement intended to optimize tidal or other currents for horizontal movement (Garrison, 1999). Either form of movement has the potential to lead to unpredictable advection vectors, differing significantly from those predicted within a model not properly parameterized to account for such behavior. Compounding matters is the limited state of knowledge of larval duration, particularly the lack of information on the megalops stage. Not only is the duration of this stage unknown, but megalops behavior, including potential for vertical migrations, frequency of such movement and average time spent at depth are not known. Failing such information, we followed the approach of Parada *et al.* (2010), ignoring the megalopa stage and focusing on only the zoeal stages with the assumption that additional advection would be of minimal consequence. This assumption is based on the scale of the study system, prevalence of sluggish, variable currents and the likelihood that megalopae would spend at least some time at greater depths, where current velocities would be

reduced relative to near-surface currents experienced by zoeae. Considering the generally north-northwest advection, were further large-scale advection to occur, we anticipate that it would lead to exposure to cooler sea surface and near-bottom temperatures and reduced exposure to groundfish and juvenile crabs, while not significantly altering sediment class at the endpoints, due to prevalence of fine-grain sediments.

Finally, laboratory investigations on thermal tolerances and preferenda, as well as temperature-mediated growth rates in both zoeae and early-stage juveniles, would be invaluable to future modeling and would help refine size-at-age estimates used in the juvenile crab index. Efforts to quantify both inter- and intra-cohort cannibalism, as functions of the prevalence of alternative prey items, gender of cannibals and the densities of both older cannibals and younger prey crabs would be of great use in determining the potential importance of this mechanism.

In conclusion, while our attempts to demonstrate a multifactor suite of interacting recruitment mechanisms for EBS Tanner crabs were not very fruitful, simpler model scenarios focusing on one or only a few factors were more successful. Although there are opportunities for the development of an improved, better informed model, within the constraints imposed by the limitations of currently available information, we propose that our results will be of value to both managers and fishery stakeholders. Our finding of an apparent relationship between NBT values >1º C and juvenile survival may be of particular value, as it suggests that future recruitment trends may be possible to predict with some accuracy based on current patterns and temperature fields forecasted from models developed by the Intergovernmental Panel on Climate Change (IPCC), as has been done previously for other species (Hollowed *et al.*, 2009).

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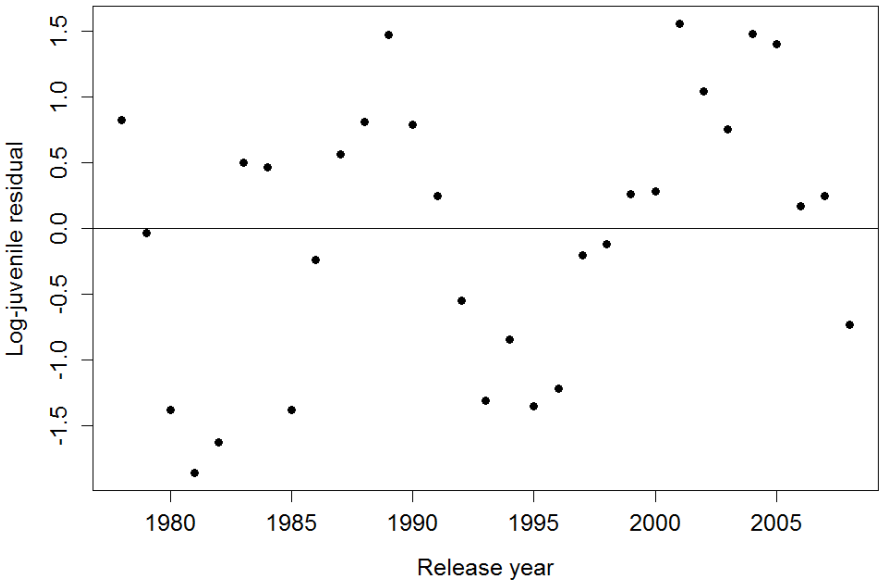

Figure 3.1. Log-juvenile residual trends. Trends in log-juvenile residuals for 1978-2008.

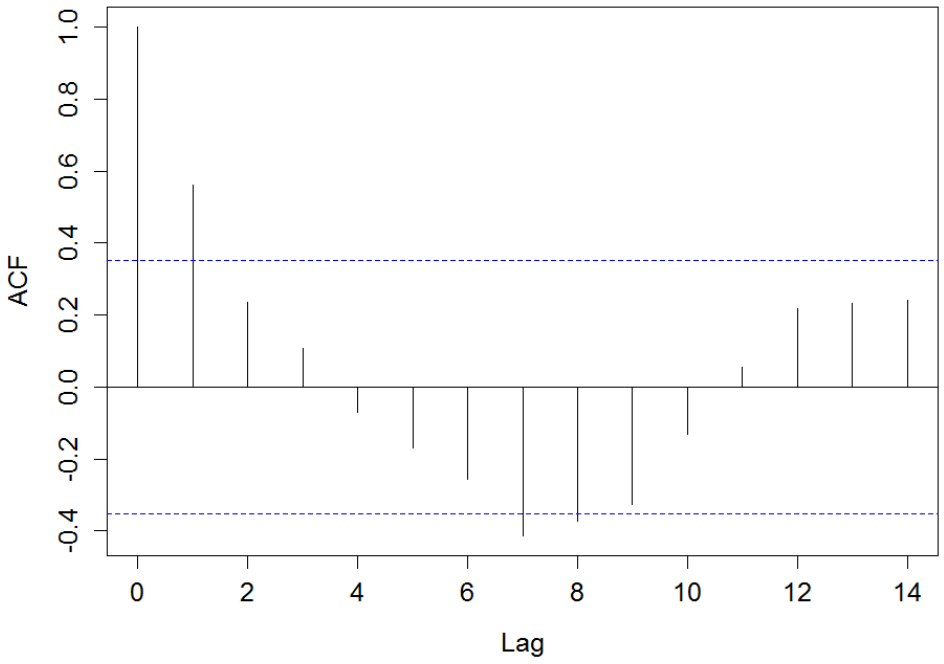

Figure 3.2. Autocorrelation function (ACF) plot. Autocorrelation function for eastern Bering Sea juvenile Tanner crabs. Dashed horizontal lines represent 95% confidence limits, with values exceeding these signifying statistically significant autocorrelation at that lag. Note significant positive autocorrelation at a lag of 1 year, and negative correlation at lags of 7 and 8 yr.

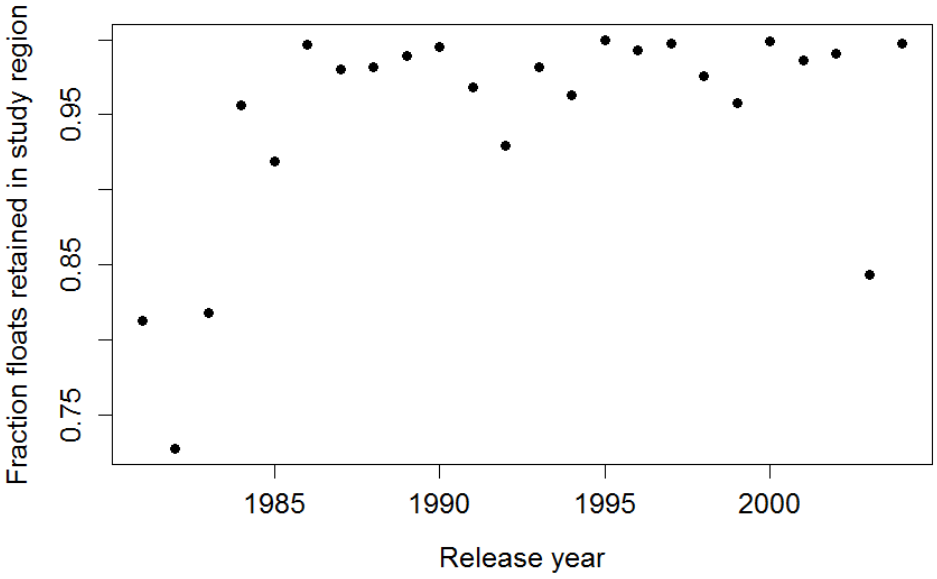

Figure 3.3. Float retention trends. Annual fraction of floats retained within the study region during 1978-2004.

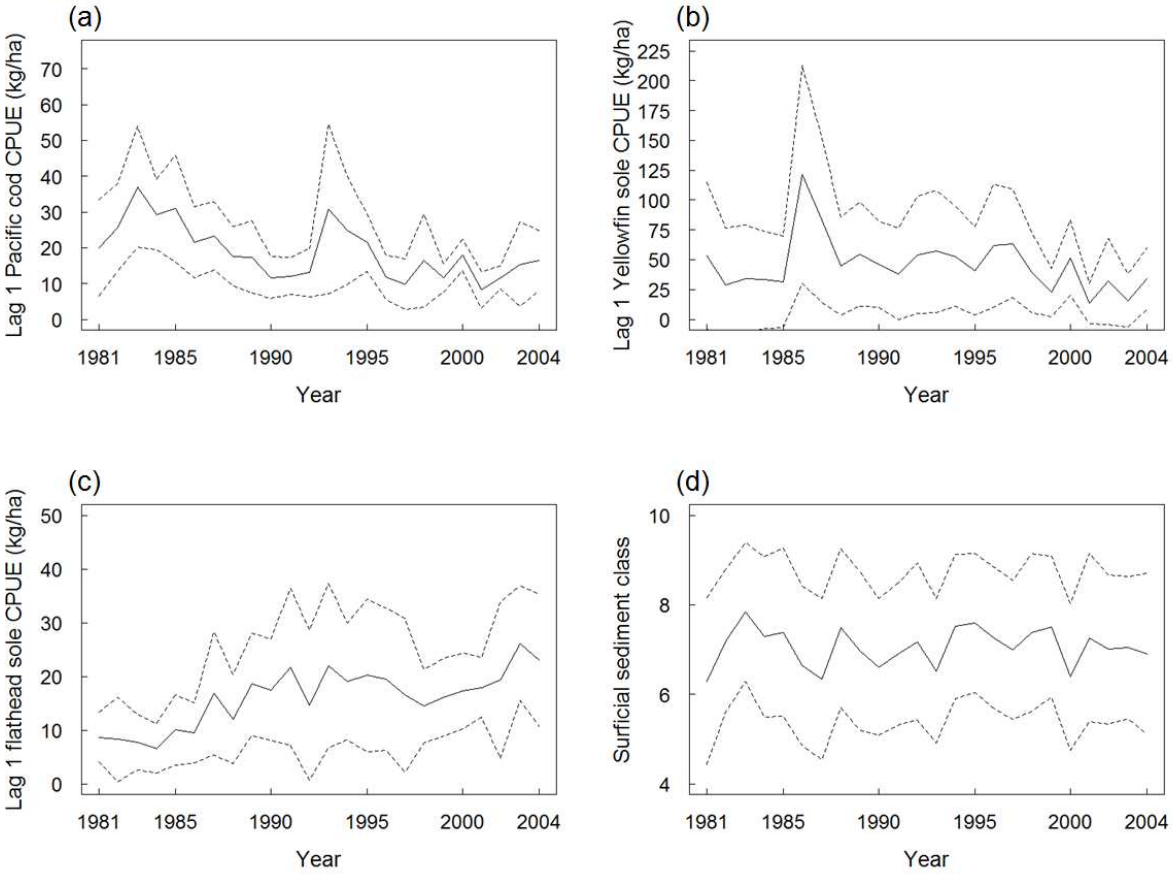

Figure 3.4. Trends in ecological conditions (I). Mean values (solid lines) of four ecological factors at float endpoints+/- 1 SD (dashed lines) for: (a) Pacific cod 1 yr after settling, (b) yellowfin sole 1 yr after settling, (c) flathead sole 1 yr after settling, and (d) surficial sediment class at the endpoints.

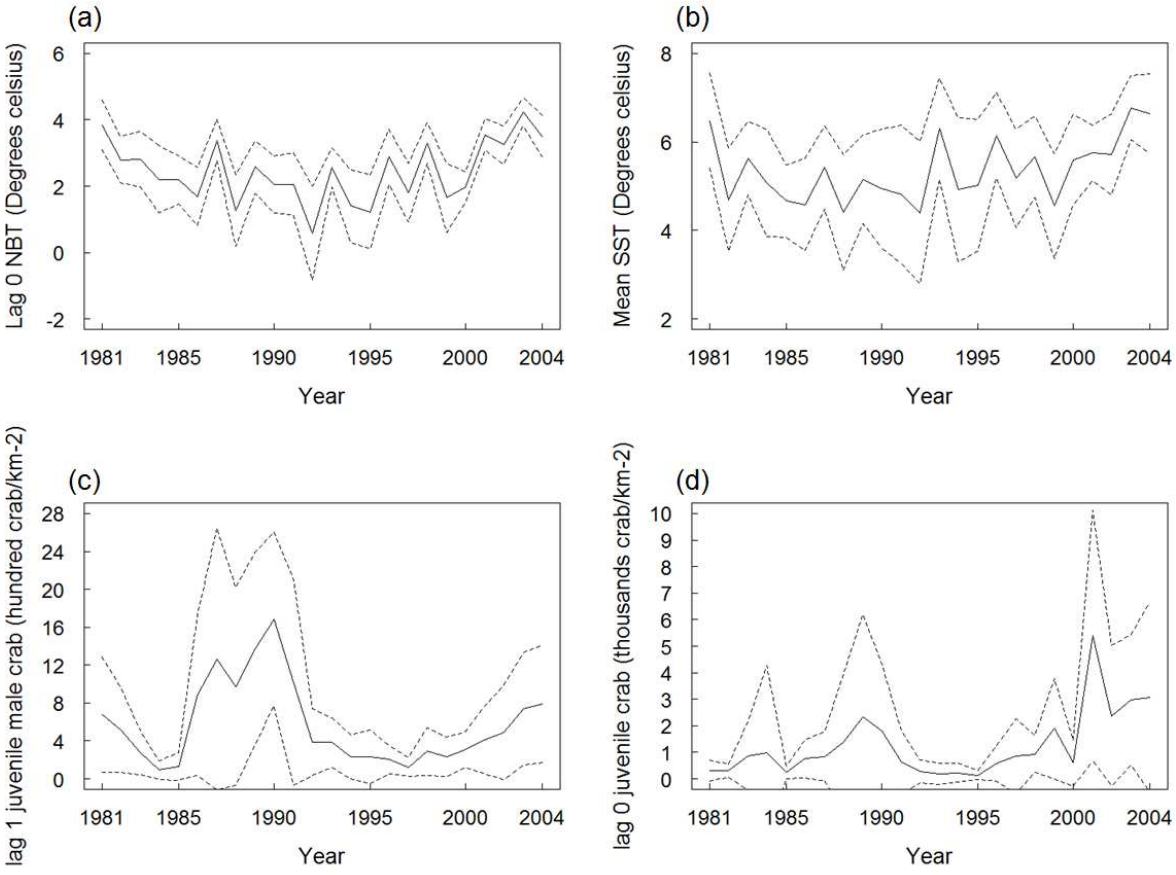

Figure 3.5. Trends in ecological conditions (II). Mean values (solid lines) of four ecological factors at float endpoints +/- 1 SD (dashed lines) for: (a) near bottom temperature (NBT) during settling year, (b) modeled sea surface temperature (SST) during advection (c) density of 70-89 mm carapace width (CW) large juvenile male crabs 1 yr after settling and (d) density of 30-50 mm CW juvenile crabs.

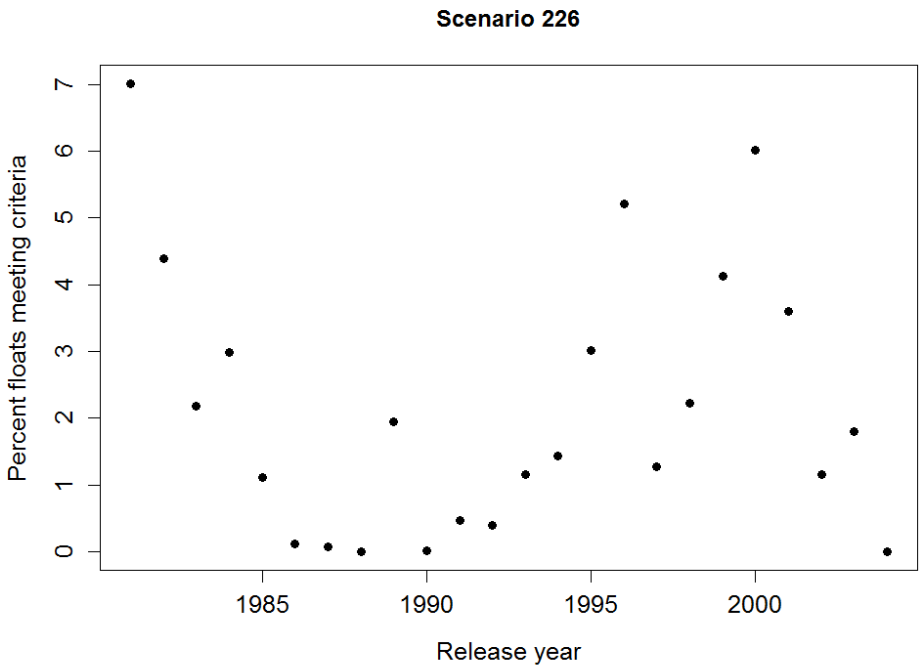

Figure 3.6. Example scenario output. Sample output derived from scenario 226, with potentially suitable conditions indicated to occur in the early 1980s and mid-late 1990s/early 2000s. Settings for this scenario were: Pacific cod < 30 kg/ha; yellowfin sole < 30 kg/ha; flathead sole <30 kg/ha; sediment class > 6; NBT > 1º C; 30-50 mm carapace width juvenile crabs <500/km^2 and 70-89 mm carapace width male crabs <400/km^2.

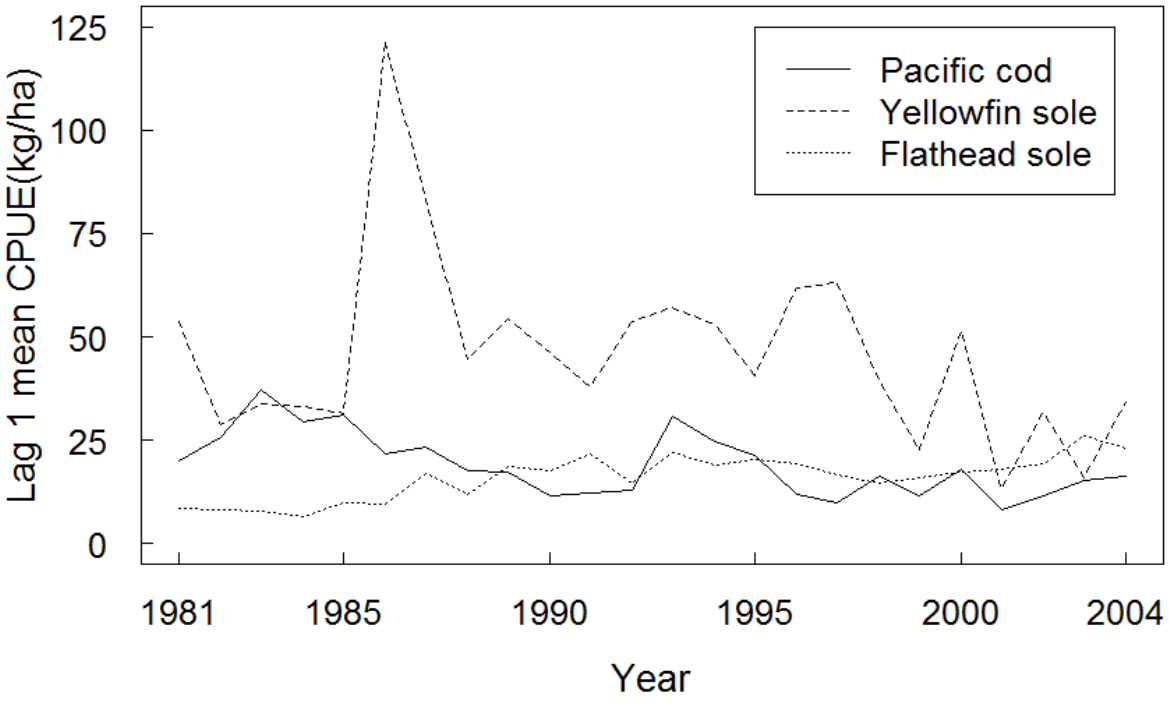

Figure 3.7. Comparison of groundfish mean CPUE. Comparison of trends in mean CPUE at endpoints for Pacific cod, yellowfin sole and flathead sole.

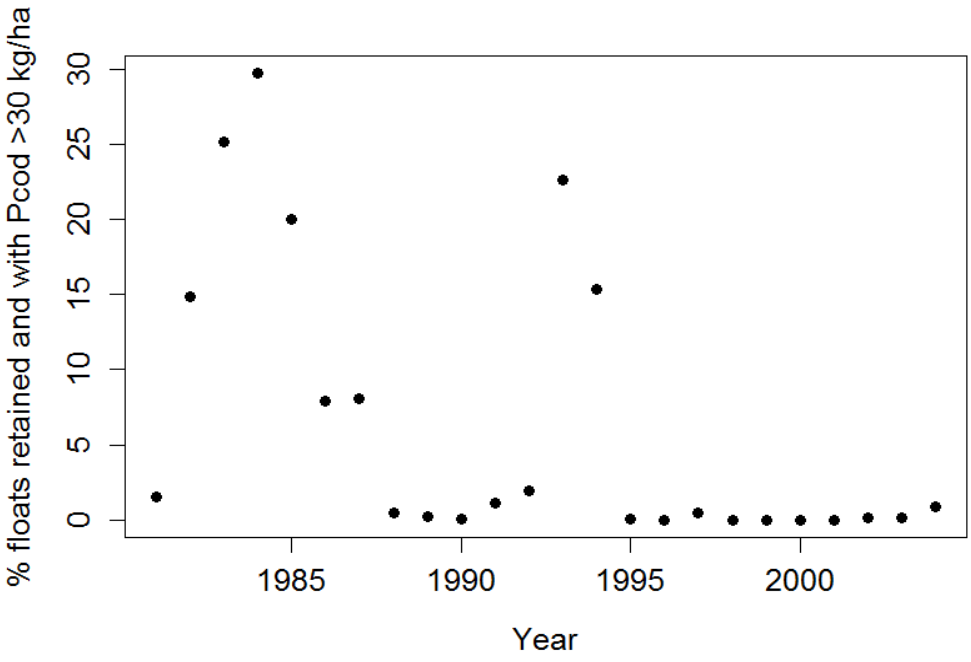

Figure 3.8. Trends in Pacific cod exposure. Time series of percentage of retained floats with estimated settling locations that experienced Pacific cod densities <30 kg/ha at lags of 1 and 2 yr post-release.

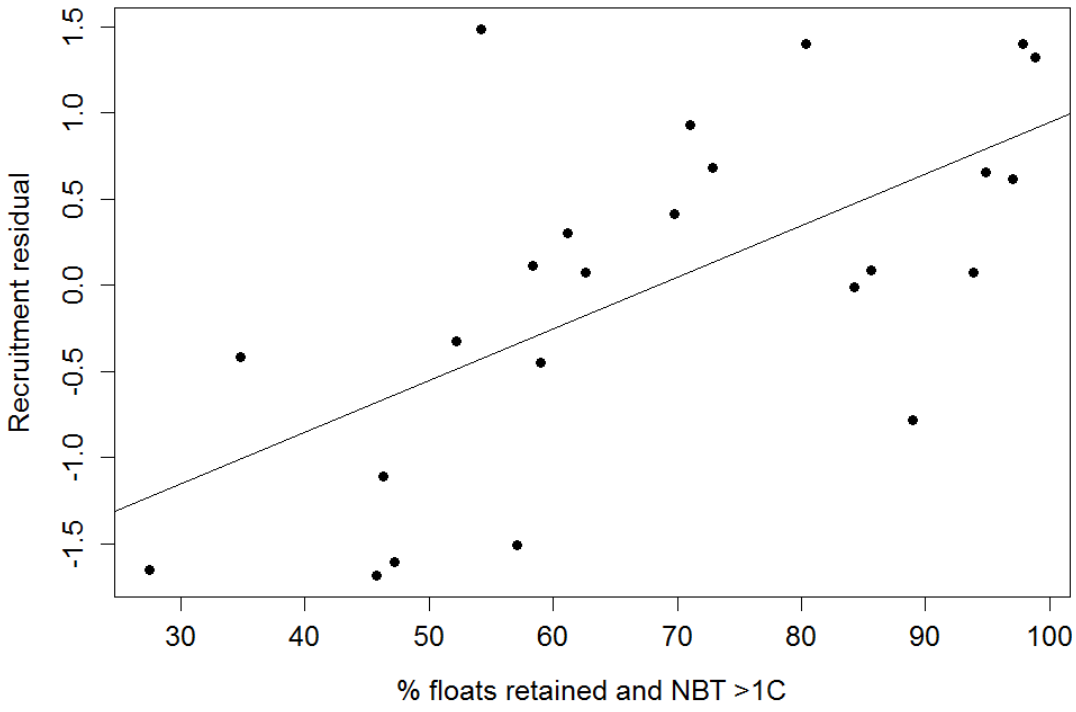

Figure 3.9. Comparison of crab recruitment vs. near bottom temperature. Comparison of observed juvenile recruitment residuals versus percentage of endpoints with NBT >1° C during each of the first 3 yr of life (lag 0, 1 and 2 yr), with least-squares linear regression line (r^2 = 0.372, p = 0.045).

Table 3.1. Date of first and final model float release by year.

Year	First day of release	Final day of release
1978	17-Apr	4-Jun
1979	17-Apr	2-Jun
1980	17-Apr	3-Jun
1981	17-Apr	2-Jun
1982	17-Apr	6-Jun
1983	17-Apr	3-Jun
1984	17-Apr	3-Jun
1985	27-Apr	26-May
1986	27-Apr	22-May
1987	27-Apr	25-May
1988	27-Apr	25-May
1989	17-Apr	2-Jun
1990	17-Apr	6-Jun
1991	17-Apr	4-Jun
1992	27-Apr	26-May
1993	17-Apr	27-May
1994	17-Apr	3-Jun
1995	17-Apr	3-Jun
1996	17-Apr	31-May
1997	27-Apr	25-May
1998	27-Apr	23-May
1999	27-Apr	25-May
2000	17-Apr	27-May
2001	17-Apr	27-May
2002	27-Apr	25-May
2003	17-Apr	2-Jun
2004	17-Apr	27-May

Table 3.2. Thresholds for individual factors. List of alternate threshold values used in gauntlet analyses by factor. Factors are: Pcod, Pacific cod in kg/ha; FHS, flathead sole in kg/ha; Yfin, yellowfin sole in kg/ha; Sed, sediment class; NBT, near bottom temperature in °C; SST, sea surface temperature in °C; Juv, 30-50 mm carapace width (CW) Tanner crab in crab/km^2; Lrg_crab, 70-89 mm CW male crab in crab/km^2. The numerals (0, 1 and 2) associated with each factor denote lags of 0, 1 and 2 yr post hatch. For NBT, "< or >" denotes that value was used as both an upper and lower threshold.

Factor	**Lags**	**Thresholds**
Pcod	1, 2	<10, <20, <30, <40, <50, <8, <100
FHS	1, 2	<10, <20, <30, <40, <50, <8, <100
Yfin	1,2	<10, <20, <30, <40, <50, <8, <100, <120, <140
Sed	0	>4, >5, >6, >7, >8
NBT	0, 1, 2	< or >1, >1.5, >1,75, < or >2, >2.25, >2.75, < or >3, >3.75,< or >4, < or >5
SST	0	>2, >3, >4, >5
Juv	0,1	<250, <400, <600, <700, <800, <1000, <1200, <1600, <2000
Lrg_crab	1, 2	<250, <300, <400, <450, <500, <600, <700, <800, <1000, <1200 <1600, <2000

Table 3.3. Statistically significant correlations. Correlations between scenario output and juvenile recruitment residuals, factors, and factor thresholds for all statistically significant ($\alpha = 0.05$) scenarios. Pcod, Pacific cod in kg/ha; FHS, flathead sole in kg/ha; Yfin, yellowfin sole in kg/ha; Sed, sediment class ; NBT, near bottom temperature in °C; SST, sea surface temperature in °C; Juv, 30-50 mm carapace width (CW) Tanner crab in crab/km^2; Lrg_crab, 70-89 mm CW male crab in crab/km^2. The numerals (0, 1 and 2) after the factors denote lags of 0, 1 and 2 yr post hatch.

Scenario	Correlation	Factor	
1	0.407	SST >3	
2	0.481	SST >4	
44	0.533	FHS1 <30	
45	0.455	FHS2 <40	
80	-0.421	Juv0 <400	
81	-0.408	Juv0 <600	
87	-0.485	Juv1 <400	
88	-0.446	Juv1 <600	
90	-0.403	Juv1 <1000	
94	-0.484	Juv0 <400	Juv1 <400
95	-0.483	Juv0 <600	Juv1 <600
96	-0.489	Juv0 <800	Juv1 <800
97	-0.496	Juv0 <1000	Juv1 <1000
98	-0.471	Juv0 <1200	Juv1 <1200
99	-0.427	Juv0 <1600	Juv1 <1600
101	-0.401	Juv0+Juv1 <400	
102	-0.451	Juv0+Juv1 <600	
103	-0.429	Juv0+Juv1 <800	
104	-0.429	Juv0+Juv1 <1000	
105	-0.451	Juv0+Juv1 <1200	
106	-0.401	Juv0+Juv1 <1600	
139	-0.478	NBT2 <1	

Table 3.3 continued

Scenario	Correlation	Factor						
144	0.612	NBT0 >1	NBT1 >1	NBT2>1.0				
164	0.431	Pcod <50	Yfin1 <50	FHS1<50	Pcod2 <50	Yfin2 <50	FHS2 <50	Sed >8
165	0.437	Pcod <80	Yfin1 <80	FHS1 <80	Pcod2 <80	Yfin2 <80	FHS2 <80	Sed >8
665	0.513	Juv0 >600	Juv1 >600					
666	0.521	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	Juv0 >600	Juv1 >600		
667	0.603	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	SST >2.0			
668	0.581	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	SST >3.0			
669	0.553	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	SST >4.0			
670	0.561	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	SST >2.0			
671	0.541	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	SST >3.0			
672	0.529	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	SST >4.0			
673	0.431	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	SST >3.0	Lrg_crab_1 <600	Lrg_crab_2 <600	
674	0.434	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	SST >4.0	Lrg_crab_1 <600	Lrg_crab_2 <600	
675	0.440	NBT0 >2.0	NBT1 >2.0	NBT2 >2.0	SST >4.0	Lrg_crab_1 <600	Lrg_crab_2 <600	
676	0.449	NBT0 >2.0	NBT1 >2.0	NBT2 >2.0	SST >3.0	Lrg_crab_1 <600	Lrg_crab_2 <600	
679	0.410	NBT0 >2.0	NBT1 >2.0	NBT2 >2.0	SST >3.0	Lrg_crab_1 <400	Lrg_crab_2 <400	
681	0.403	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	Lrg_crab_1 <500	Lrg_crab_2 <500		
683	0.426	NBT0 >2.0	NBT1 >2.0	NBT2 >2.0	Lrg_crab_1 <500	Lrg_crab_2 <500		
685	0.435	NBT0 >1.5	NBT1 >1.5	NBT2 >1.5	Lrg_crab_1 <600	Lrg_crab_2 <600		
686	0.451	NBT0 >2.0	NBT1 >2.0	NBT2 >2.0	Lrg_crab_1 <600	Lrg_crab_2 <600		

Table 3.4. Statistically significant autocorrelation-adjusted correlations. Statistically significant correlations between scenario output and juvenile recruitment residuals after accounting for autocorrelation, factors, and related thresholds. Factors are: SST, mean modeled sea surface temperature along float track lines; NBT, near bottom temperature. Retention within study area was incorporated into all scenarios. NBT and SST are in °C. The numerals 0, 1 and 2 denote lags of 0, 1 and 2 yr post hatch.

Scenario	Correlation	P-value	Factor			
2	0.481	0.024	SST >4.0			
139	-0.478	0.018	NBT2 <1.0			
144	0.612	0.045	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	
667	0.603	0.049	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	SST >2.0
668	0.581	0.047	NBT0 >1.0	NBT1 >1.0	NBT2 >1.0	SST >3.0

General Conclusions

Recruitment of juvenile EBS Tanner crabs in the is a complex process likely governed by interactions of multiple factors acting in concert and/or sequentially across multiple life stages, time scales and spatial extents. Thus, identification of specific mechanisms is problematic, requiring application of multiple approaches.

An approximately 12 yr cycle in juvenile abundance, corresponding to two female crab maturation cycles, is suggestive of an endogenous rhythm springing from a stock-recruit relationship. Ricker model based analyses support this, with a strong-density-dependent effect being observed. The specific mechanisms by which this effect occurs are less obvious: candidates may include both intercohort and intracohort post-settlement cannibalism, exhaustion of food resources during the zoeal phase during years of high reproductive output, or less likely, disease. However, an alternative explanation is that the apparent rhythm arises from a cyclical environmental process affecting survival to recruitment. An apparent strong density dependent stock-recruit relationship has been shown to result when environmental drivers cause recruitment to cycle with periodicity that is twice the mean generation time of a given population.

Groundfish predation may comprise an important recruitment mechanism for juvenile Tanner crabs depending on the species in question. Flathead sole, an increasingly ubiquitous species in the EBS and known crab predator demonstrates a pronounced, statistically significant negative effect at high densities. However, neither Pacific cod, long-considered likely to be a major predator of juvenile crab, nor yellowfin sole, a highly abundant species appear to comprise a significant recruitment mechanism.

Connectivity trends suggest that local retention of larvae is an important feature throughout the EBS Tanner crab population, with sustained connectivity between subpopulations being most prominent along-shelf towards the northwest. As such, local processes may play a far greater role in determining recruitment, first to the juvenile stages, and later to the adult stage, than had previously been suspected. Further, subpopulations may be far less resilient to overfishing than traditionally assumed. This is borne out by the continued lack of recovery in the population east of 166º W longitude, which our results suggest receives only limited larval subsidies from other areas. Together, these results may validate our previous observation of a stock-recruit relationship. Relative genetic homogeneity across the population, which has stymied previous genetics-based attempts to determine the existence of subpopulations, may result from infrequent anomalous transport events able to connect subpopulations across comparatively large distances.

Spatially-explicit methods have great potential for unraveling ecological relationships that may vary in both space and time. Analyses comparing spatial distributions of environmental factors against juvenile crab recruitment through biologically reasonable thresholds for each factor that might favor crab survival met with limited success at best. While more complex scenarios gave lackluster performance, simpler scenarios focusing on 1-3 factors were more successful. In basic correlation analyses, factors that were statistically significant and positively correlated with juvenile crab recruitment included near bottom temperature (NBT) values indicating endpoint locations either outside of the cold pool, or within relatively warmer portions of the cold pool (>1° C), sea surface temperatures (SST) >2º C, low to moderate densities of flathead sole and 70-89 mm carapace width (CW) large juvenile male

crab, and high densities of 30-50 mm CW juvenile crab. After adjusting statistical significance for autocorrelation in the juvenile crab recruitment series, however, only NBT and SST were statistically significant, and SST only when paired with NBT. Findings for NBT and SST provide support for the hypothesis that temperature is an important environmental recruitment factor for EBS Tanner crab. While initial findings for flathead sole and 70-89 mm CW crab appear to offer some support for the hypothesis that predation and cannibalism by older crab, respectively, are important recruitment mechanisms, the apparent relationships seem to be driven by autocorrelation in juvenile crab recruitment trends. Autocorrelation is most likely responsible for the observed relationship between high densities of 30-50 mm CW crab at the model endpoints, and juvenile crab recruitment. Perhaps explaining our poor statistical results with Pacific cod, these analyses indicate a pronounced decline in exposure to Pacific cod since the late 1980s, suggesting that, while this species may have once comprised an important recruitment mechanism, this may no longer be the case, at least within the temporal bounds of the work presented in this dissertation.

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Appendix A:

Additional Statistical Analyses Not Reported in Chapter 1

Introduction

In addition to the statistically significant recruitment factors reported in Chapter 1, I investigated several other factors that generally yielded non-significant or inconclusive results, and were thus excluded from that chapter. These included both near-bottom temperature (NBT) and sea-surface temperature (SST), cannibalism by large (70-89 mm carapace width) juvenile male crabs and mean wind vector using simple linear regression. In addition I investigated these factors in conjunction with indices for the winter Arctic Oscillation (AOw) and summer Pacific Decadal Oscillation (PDOs) through multiple regression modeling. For the sake of completeness, I briefly outline the hypotheses and analytical methods, and provide summaries of these results here. Due to the poor results for these factors I do not provide in-depth analysis of these results.

Hypotheses

I tested the following null hypotheses:

H_{01}: Survival of juvenile Tanner crabs is not enhanced by wind-driven larval advection.

H_{02}: Survival of juveniles is not adversely affected by cannibalistic older and larger crabs.

H_{03}: Development and survival of embryonic Tanner crabs are not adversely affected by exposure to the especially cold NBT associated with the cold pool.

H_{04}: Survival of juvenile Tanner crabs is not negatively affected by exposure to cold NBT (<2°C) associated with the cold pool.

H_{05}: Survival of zoeal stage Tanner crabs is not favored by warmer SSTs during the planktic zoeal stages.

H_{06}: Recruitment strength is not related to the AOw or PDOs, both of which serve as indices for long-term climatic patterns in the eastern Bering Sea.

Methods

Data Sets

Cannibalism

To test for evidence of a cannibalism effect on recruitment of early stage juvenile Tanner crabs by older, larger individuals, the stock-recruit (S-R) residuals were regressed against annual abundance estimates for large juvenile male Tanner crabs (70-89 mm carapace width) at lags of 0, 1 and 2 yr post-release. In addition 2- and 3-yr running averages of large crab abundance were also considered.

Sea Surface Temperature

Extended reconstructed SST version 3b (ERSST v3b) model data were obtained from the National Climate Data Center (http://www.ncdc.noaa.gov/oa/climate/research/sst/ersstv3.php). The ERSST v3b is the latest version of an SST reconstruction covering the time period from 1854 to the present. In comparison to v3a, v3b dispenses with the use of satellite observations, which were found to cause a small residual cold bias (~0.01° C) in temperature estimates due to interference from cloud cover, while retaining adjustments for effects of sea ice concentration on SST, improved statistical methods and the *in situ* SST data of v3a (Smith *et al.* 2008). Data

comprise super-observations on a 2° x 2° grid scale. Although observations at this scale may dampen out local-scale variability, this data set remains useful for larger scale applications and has been employed in similar studies in this region (Mueter *et al.* 2011). Monthly, bi-monthly, and seasonal anomalies from the long-term (April-July 1978-2005) mean were calculated and lagged for their hypothesized effect during the zoeal phase (lag 0 yr).

Near-Bottom Temperature

Summer NBTs in the EBS region for 1978-2008 were obtained from the NMFS summer trawl survey database. Annual mean NBT was estimated from all sampled survey stations to provide an index of interannual variability across the EBS region. Annual anomalies from the 1978-2005 mean were calculated for each year and lagged for effects during the embryonic stage (lag -1 yr), immediately following settling (lag 0 yr), and the 1st and 2nd years following settling (lag +1 yr and +2 yr. Also, 2- and 3-yr running averages of anomalies were considered as a proxy for cumulative temperature effects..

Winds

Data for estimated wind vectors at a height of 10 m were obtained from an online database for the NCAR/NCEP Reanalysis model maintained by NOAA/OAR/ESRL PSD at http://www.esrl.noaa.gov/psd/. This data set was generated using an advanced weather prediction model with supplementary field observations obtained from surface, atmospheric and orbital sources. The procedural consistency that has been used in the reanalysis makes the data set excellent for examining interannual variability, and it has been found to correspond very well to field observations obtained from sources that were not used in its generation (Bond and Adams 2002, Ladd and Bond 2002). The data were provided as daily means for zonal and

meridional components on a ~1.9° Gaussian grid; data for this study were bounded by 56.189° N to 58.093° N and 161.250° W to 172.5° W. Monthly, bimonthly and full-period average vector components for May-July were then resolved at 15° increments from 0° (northerly, N) to 180° (southerly, S) and were lagged for effect during the zoeal phase (lag 0 yr).

Climate Indices

In light of the observed cyclical trends in all S-R residual series, the PDOs and AOw were also obtained from NOAA (http://www.beringclimate.noaa.gov/) to examine potential relationships with complex long-term climatic patterns. Due to uncertainty in potential mechanisms through which they may influence Tanner crabs, these were only used in multiple regression analyses on an exploratory basis, and were lagged for effect during only the zoeal phase (lag 0 yr).

Statistical Analyses

Simple Linear Regression Models

For analyses of environmental effects on survival and recruitment of Tanner crabs I first adjusted variability in log-transformed survival rates for possible density dependence. That is, I computed residuals from a Ricker S-R relationship by fitting a model of $\ln\left(\frac{R}{S}\right)$ as the response variable on abundance estimates for reproductive females (SC 3 + SC 4) as the explanatory variable (eq. A.1):

$$ln\left(\frac{R}{S}\right) = \alpha + \beta S + \varepsilon_t, \qquad \text{(eq. A.1)}$$

where R = juvenile crab recruits, S = reproductive female crab spawners, α = recruits-per-spawner at very low population sizes, β = measure of rate of decrease in the ratio of recruits to

spawners as S increases and ε_t = the autocorrelated error term. These S-R residuals were then used as response variables to examine possible effect of environmental variables and cannibalism on recruitment. Comparison of S-R residuals against the recruitment anomalies used in the final analyses for Chapter 1 show very similar variability (r^2 = 0.81, EBS group), thus I did not repeat the analyses presented here using recruitment anomalies. Stock-recruit models were considered with lags of 2, 3 and 4 yr; lag 3 models were selected for subsequent use on the basis of both strength of fit and prior understanding of average size at age for juvenile crab. The S-R models were fitted using generalized least squares (GLS) regression procedures, including specification of the AR(1) process identified in our autocorrelation analysis. For the purpose of comparison, models not incorporating autocorrelation were also fitted for both NBT and large juvenile male crab.

To investigate potential relationships between biophysical factors and Tanner crab recruitment, model residuals from the lag-3 S-R fits for each group (eastern, western, and total EBS) were regressed separately against each factor at biologically reasonable lags. Two alternate relationships were explored, the simplest being simple linear regressions (eq. A.2):

$$R = \beta_0 + \beta_1 X + \varepsilon_t, \qquad \text{(eq. A.2)}$$

where R = the S-R residuals, β_0 and β_1 are model parameters, X = the environmental factor of interest and ε_t = the autocorrelated error term. In cases in which residual diagnostics indicated apparent trends that could not be accounted for by simple linear trends, quadratic terms were included to allow for curvilinearity in the model relationship (eq. A.3):

$$R = \beta_0 + \beta_1 X + \beta_2 X^2 + \varepsilon_t, \qquad \text{(eq. A.3)}$$

where β_2 is an additional model parameter, X^2 = the square of the population estimate to allow for curvature, and other terms are as in eq. (6). The GLS procedures and the AR(1) autocorrelation process were used while statistical significance was evaluated at $\alpha = 0.05$ using two-tailed *t*-tests. All analyses were completed using R version 2.14 (R Development Core Team 2005).

Multiple Regression Models

For the multiple regression models, variables were selected from those that were at least weakly significant ($p < 0.10$) in simple linear regressions, although factors with a strong theoretical basis or which were significant in previous studies were also included to explore the possibility of stronger interactive effects that were not revealed by simple linear regression analyses. Consistent with Rosenkranz et al. (1998, 2001), only the May-June mean wind component was analyzed to reduce the possibility of spurious correlations and because these months represent the main pelagic larval period (Rosenkranz et al. 1998, 2001). The dependent variable was the lag-3 S-R residual series calculated for each group (eastern, western, and EBS). In initial models, residual series from S-R models both including and excluding the highly anomalous 1982 female/1985 juvenile data point were employed. Following consideration of the effects on model fit of including this pair, and due to concerns about the female estimate (see Chapter 1, pp. 14-15 for full discussion), only the "edited" residual series from the S-R models for each group with this pairing dropped ere used. To begin, linear models were fitted using step-wise model selection procedures to select the strongest candidates for further analyses.

To allow for autocorrelation, GLS models were then fitted for each group while using the linear model results to guide variable selection. I began with simple linear regression models of the "best" explanatory variables for that group as identified by the linear model analyses. Variables were lagged appropriately and manually added until a full model had been built including all variables previously identified as potential candidates. Interaction terms were included, if deemed biologically reasonable to test for interactions among the variables.

Variables examined in multiple regression analyses included the mean 60°, 75°, 90°, 150°, 175° and 180° wind components for May-June, flathead sole biomass, PDOs, AOw and May-June mean SST, in addition to interaction terms for wind component * flathead sole biomass and wind component * AOw. For each model I calculated the small- sample Akaike Information Criterion (AICc), due to the relatively short residual time series (n = 28) relative to the number of parameters being investigated. As with the simple linear regression analyses, statistical significance for individual parameters was determined at $\alpha = 0.05$ using t-tests. Model suitability was determined based on the significance level of the variables, inspection of residual plots and reduction in AICc relative to the simple regression model with the lowest AICc value.

Results

Cannibalism of Juveniles by Larger Males

Regressions of abundance of male crabs > 70 mm CW (independent variable) and S-R residuals (dependent variable) lagged 0, 1 and 2 yr, as well as 2- and 3-yr running averages failed to reveal significant relationships when autocorrelation was accounted for (Table A.1). In models without autocorrelation terms, lag 0 and 1 yr models were significant for the EBS

group, while for both the EBS and western groups, models incorporating 2-yr running averages for the first 2 yr of life were significant. For the eastern group, only the lag 0 model was significant (Table A.1). Scatterplots are also suggestive of weak negative relationship at these lags (Fig. A.1, A.2). Autocorrelation was significant in all models for the western and EBS groups, but was not significant in eastern group models (Table A.1).

Effects of Mean Near-Bottom Temperature on Embryo Development and Juvenile Stages

One statistically significant ($p = 0.02$) negative relationship between recruitment and the running average of mean bottom temperature during the first 3 yr of life was observed in a quadratic model for the western group (Table A.2). However, examination of a scatterplot of these data revealed two outliers on the lower right side of the plot, representing the 1978 and 1979 pseudocohort S-R residuals (Fig. A.3). Removal of these data points resulted in non-significance ($p = 0.15$). Model output and scatterplots for other regions and lags did not indicate any other relationships with NBT.

Favorable Sea Surface Temperature during Larval Stages

No statistically significant relationships between sea surface temperature during the zoeal stage and juvenile Tanner crab recruitment were observed (Table A.3).

Favorable Winds for Advection

Regression of mean vector wind components at 15° increments from 0° north to 180° south failed to demonstrate a significant relationship between these components and the S-R residuals for the EBS and western groups (Table A.4, A.5). For the eastern group, the May-June 150° and 165° components were statistically significant ($p < 0.05$) and positively related to the S-R residuals (Table A.6, Fig. A.4). Notably, the apparent relationships were generally

driven by a few highly influential data points. When these were removed, the relationships became non-significant.

Multiple Regression Models

There was significant variability in both "best" reduced model and "best" full model, depending on the study group in question. For both the EBS and western groups, the "best" reduced model, incorporated only flathead sole at lags of 1 yr (EBS group) and 2 yr (western group, Table A.7). For the eastern group, the best reduced model incorporated only the AOw lagged for effect during the larval phase (Table A.7). Pronounced trends were however observed in model residuals, suggesting these models were not able to account for significant recruitment variability Figs A.5a, A.6a, A.7a).

For all three groups the "best" full model incorporated wind components (EBS, -90º; eastern, 90º, western; -75º), and flathead sole total biomass (TBM) (EBS and eastern group, lag 1; western group, lag 2) (Table A.7). In addition the EBS full model incorporated the AOw and PDOs indices, while the eastern group model added only the AOw index, and the western group model, only the PDOs index (Table A.7). However, as in the baseline models, trends were still observed in model residuals, supporting the conclusion that these models were unable to fully account for variability in crab recruitment (Figs A.5b, A.6b, A.7b).

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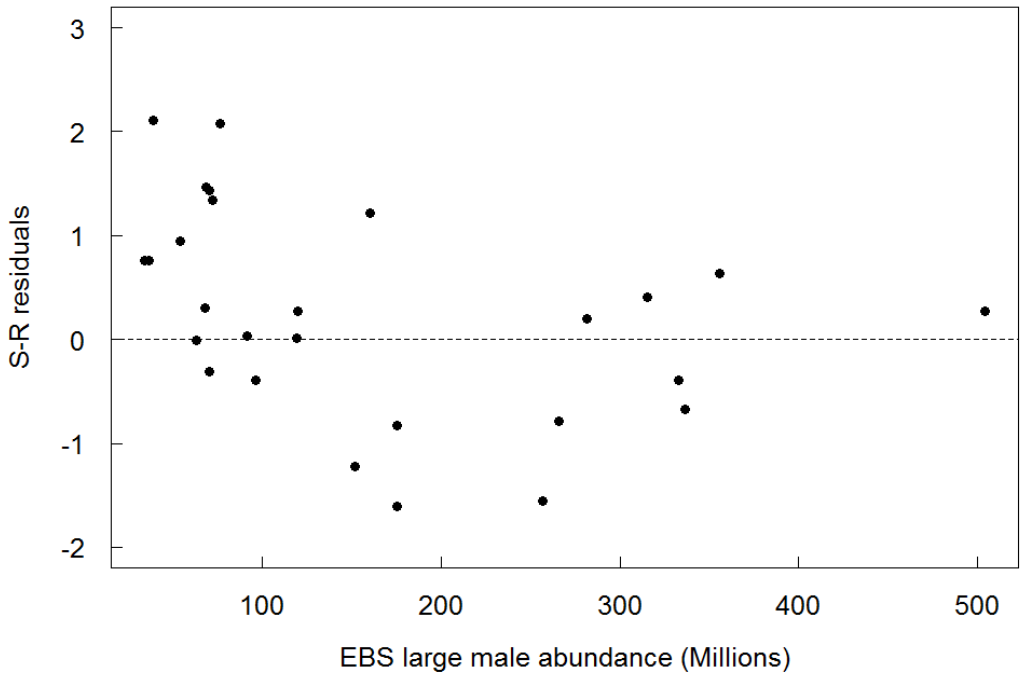

Figure A.1. Stock-recruit residuals vs. large subadult male crab abundance (lag-0 yr). Stock-recruit (S-R) residuals for the eastern Bering Sea (EBS) versus large (70-89 mm carapace width) subadult male abundance (millions) during hatching year (lag-0 yr) for cannibalism immediately after settling.

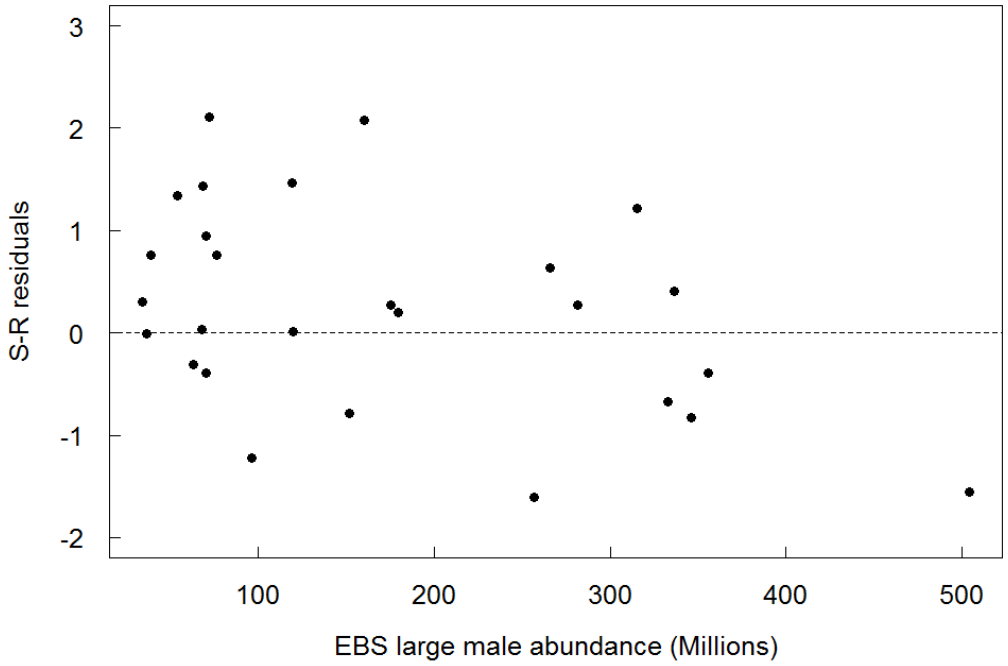

Figure A.2. Stock-recruit residuals vs. large subadult male crab abundance (lag-1 yr). Stock-recruit (S-R) residuals for the eastern Bering Sea (EBS) versus large (70-89 mm carapace width) subadult male crab abundance lagged 1 yr after crab hatching for cannibalism during the first juvenile year.

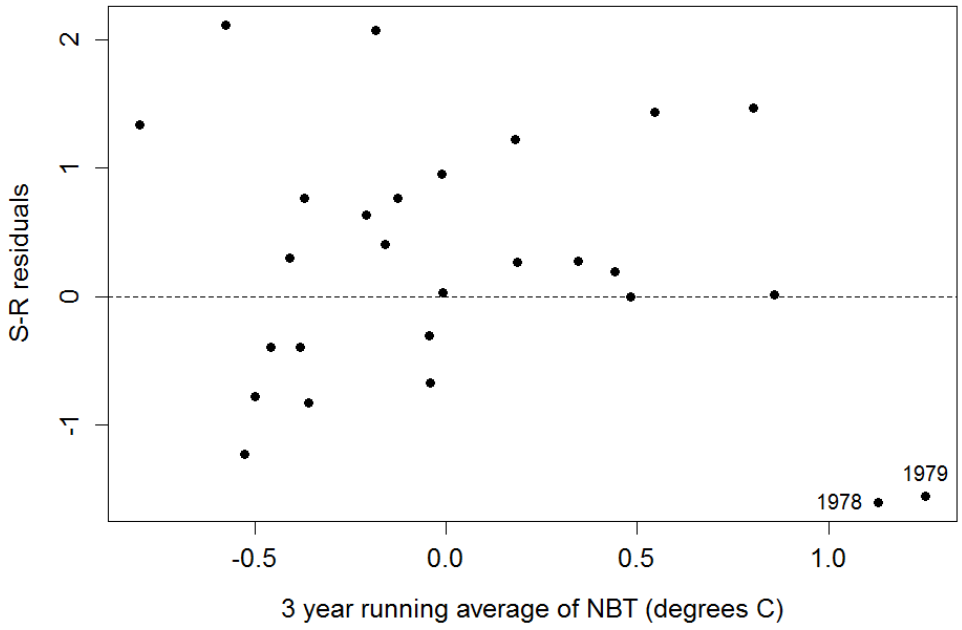

Figure A.3. Stock-recruit residuals vs. near-bottom temperature. Stock-recruit (S-R) residuals lagged 3 yr versus the 3-yr running average of near-bottom temperature (NBT) for the eastern Bering Sea (EBS).

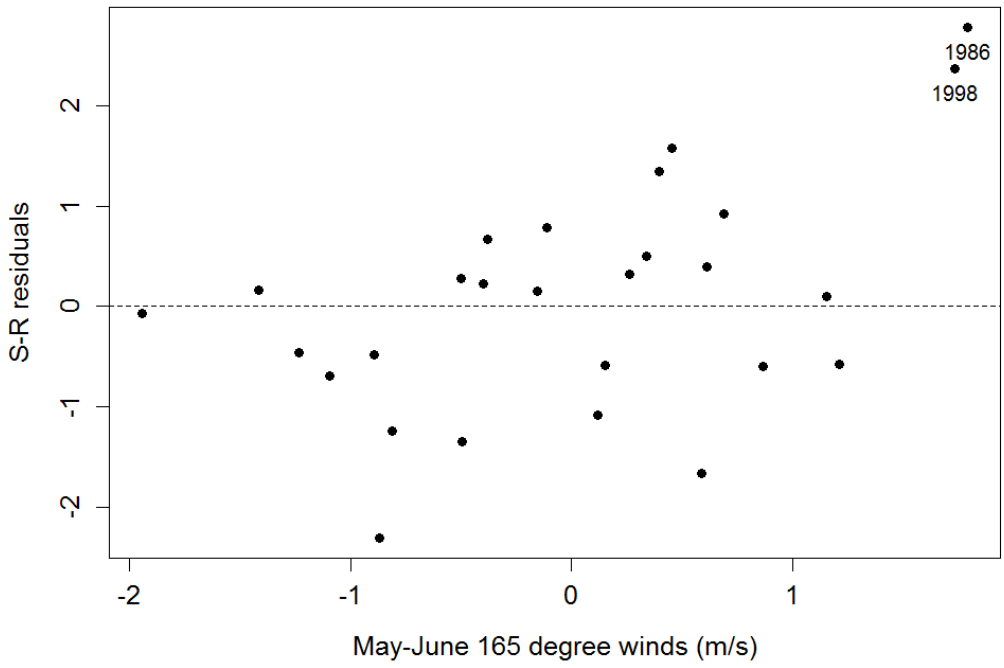

Figure A.4. Eastern group stock-recruit residuals vs. 165^{o} winds. Stock-recruit (S-R) residuals for the eastern group versus the hatch year (0 yr lag) 165° (south-southeast) wind vector component (m/s). Note the data points for 1986 and 1998 year classes, which appear to drive the observed relationship.

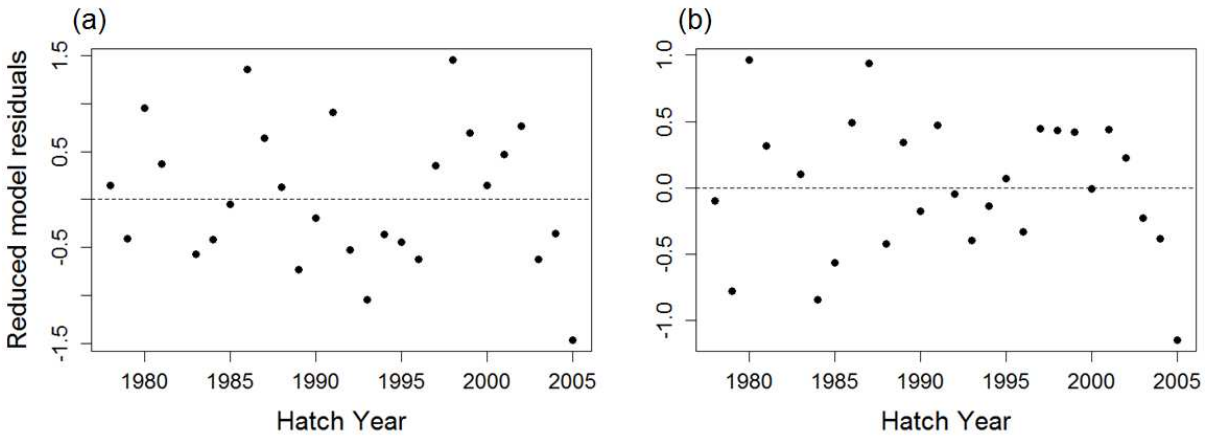

Figure A.5. Best model residuals by hatch year for the eastern Bering Sea. Residuals from the best-fitting (a) reduced model and (b) full model, for the eastern Bering Sea by hatch year over 1978-2005. Note the cyclic residual pattern in (a).

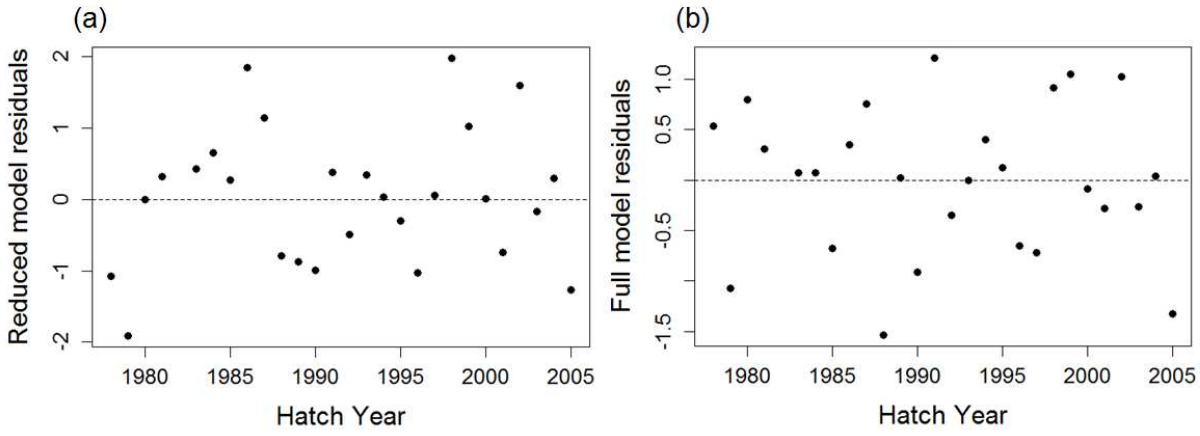

Figure A.6. Best model residuals by hatch year for the eastern area. Residuals from the best-fitting (a) reduced model and (b) full model for the eastern study area by hatch year over 1978-2005. Note the cyclic pattern in residuals in (a).

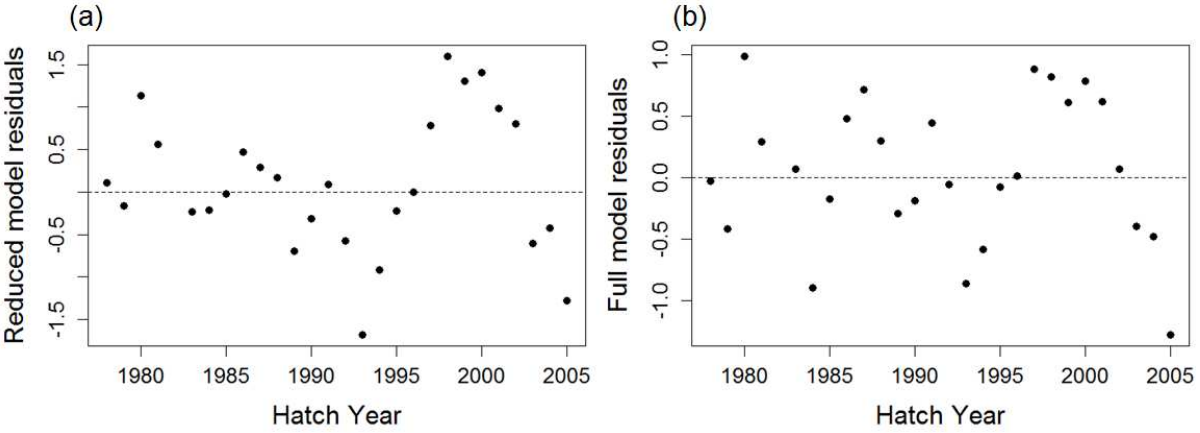

Figure A.7. Best model residuals by hatch year for the western area. Residuals from the best-fitting (a) reduced model and (b) full model, for the western study area by hatch year over 1978-2005. Note the cyclic pattern in residuals present in both, and particularly in (a).

Table A.1. Statistics for cannibalism models. P-values for cannibalism models by region and lag with autocorrelation terms unless specified. No AR = autocorrelation not incorporated, RA3 = 3-yr running average for effect during intervening juvenile years, RA2(1) = 2-yr running average lagged for effect beginning during 1st year post-hatch, RA2(2) = 2-yr running average lagged for effect beginning during the 2nd year post-hatch. Where given, +/- indicates sign of statistically significant relationships. Signs are not given for non-significant models.

Level	East		West		EBS	
	x_i	φ	x_i	φ	x_i	φ
Lag 0	0.08	0.18	0.41	0.88	0.97	0.83
Lag 0 no AR	0.01(-)		0.08		0.01(-)	
Lag 1	0.55	0.25	0.32	0.85	0.20	0.79
Lag 1 no AR	0.36		0.09		0.03(-)	
Lag 2	0.90	0.29	0.90	0.87	0.90	0.83
Lag 2 no AR	0.87		0.36		0.30	
RA3	0.89	0.29	0.50	0.85	0.45	0.81
RA3 no AR	0.86		0.39		0.32	
RA2(1)	0.23	0.21	0.89	0.86	0.36	0.78
RA2(1) no AR	0.13		0.05(-)		0.01(-)	
RA2(2)	0.94	0.29	0.96	0.87	0.93	0.83
RA(2) no AR	0.82		0.79		0.82	

Table A.2. Statistics for near bottom temperature models. P-values for near bottom temperature models by area, lag, and model parameter. RA3(1) = 3-yr running average lagged for intervening juvenile years, RA3(2) = as before with a polynomial term to allow for curvilinear relationship, RA3(3) = 3-yr running average lagged for effect beginning during embryonic stage, RA2(1) = 2-yr running average lagged for first 2 juvenile years, RA2(2) = 2-yr running average lagged for effect beginning during embryonic stage. Where given, +/- indicates sign of statistically significant relationships. Signs are not given for non-significant models. NA indicates that the given term was not included in that model.

Level	East			West			EBS		
	x_i	x_i^2	φ	x_i	x_i^2	φ	x_i	x_i^2	φ
Lag -1	0.96	NA	0.25	0.39	NA	0.48	0.42	NA	0.70
Lag 0	0.54	NA	0.27	0.11	NA	0.58	0.25	NA	0.69
Lag 1	0.26	NA	0.23	0.26	NA	0.62	0.89	NA	0.71
RA3 (1)	0.54	NA	0.24	0.44	NA	0.57	0.36	NA	0.70
RA3 (2)	NA	NA	NA	0.81	0.02 (-)	0.56	0.86	0.08	0.69
RA3 (3)	0.43	NA	0.23	0.64	NA	0.48	0.77	NA	0.66
RA2 (1)	0.65	NA	0.25	0.60	NA	0.55	0.19	NA	0.68
RA2 (2)	0.60	NA	0.30	0.60	NA	0.55	0.19	NA	0.68

Table A.3. Statistics for monthly sea surface temperature models. P-values for sea surface temperature models by group and period over which given vector mean was calculated, with autocorrelation terms. Where given, +/- indicates sign of statistically significant relationships. Signs are not given for non-significant models. NA indicates that the given term was not included in that model.

	East		West		EBS	
Average	x_i	φ	x_i	φ	x_i	φ
April	0.61	0.25	0.11	0.59	0.44	0.71
May	0.92	0.23	0.13	0.58	0.10	0.83
June	0.99	0.24	0.83	0.55	0.13	0.73
July	0.46	0.29	0.79	0.56	0.56	0.72
April-May	0.84	0.24	0.10	0.58	0.19	0.70
May-June	0.97	0.24	0.37	0.57	0.08	0.72
June-July	0.66	0.27	0.79	0.56	0.29	0.73
April-July	0.71	0.26	0.28	0.59	0.18	0.72
May-July	0.77	0.26	0.47	0.58	0.17	0.72

Table A.4. Statistics for eastern Bering Sea wind models. P-values from wind models for the eastern Bering Sea by vector angle and period over which given vector means were calculated. Where given, +/- indicates sign of significant model relationships. Signs are not given for non-significant models.

	EBS					
Angle of component	May-June	June-July	May-July	May	June	July
0° (North)	0.24	0.78	0.46	0.30	0.77	0.31
15°	0.33	0.77	0.50	0.33	0.89	0.51
30°	0.44	0.81	0.58	0.37	0.97	0.77
45°	0.58	0.87	0.66	0.42	0.84	0.98
60°	0.74	0.92	0.75	0.50	0.72	0.88
75°	0.94	0.97	0.83	0.62	0.65	0.77
90° (East)	0.84	0.98	0.92	0.82	0.59	0.67
105°	0.60	0.95	0.99	0.86	0.57	0.59
120°	0.38	0.92	0.88	0.52	0.56	0.51
135°	0.24	0.89	0.75	0.34	0.58	0.43
150°	0.18	0.85	0.62	0.29	0.62	0.35
165°	0.19	0.82	0.50	0.29	0.68	0.28
180° (South)	0.24	0.78	0.46	0.30	0.77	0.31

Table A.5. Statistics for western area wind models. P-values from wind models for the western area by vector angle and period over which given vector means were calculated. Where given, +/- indicates sign of statistically significant relationships. Signs are not given for non-significant models.

	West					
Angle of component	May-June	June-July	May-July	May	June	July
0° (North)	0.40	0.66	0.36	0.47	0.70	0.80
15°	0.55	0.90	0.52	0.46	0.99	0.84
30°	0.73	0.80	0.72	0.47	0.64	0.89
45°	0.94	0.63	0.92	0.48	0.39	0.94
60°	0.85	0.54	0.90	0.51	0.27	0.97
75°	0.65	0.50	0.76	0.58	0.23	0.99
90° (East)	0.48	0.48	0.64	0.71	0.22	0.98
105°	0.35	0.47	0.53	0.95	0.23	0.95
120°	0.27	0.47	0.44	0.78	0.26	0.93
135°	0.24	0.47	0.36	0.60	0.30	0.90
150°	0.25	0.49	0.31	0.52	0.38	0.87
165°	0.30	0.54	0.30	0.48	0.50	0.83
180° (South)	0.40	0.66	0.36	0.47	0.70	0.80

Table A.6. Statistics for eastern area wind models. P-values from wind models for the eastern area by vector angle and period over which given vector means were calculated. Where given, +/- indicates sign of statistically significant relationships. Signs are not given for non-significant models.

Component angle	May-June	June-July	May-July	May	June	July
0° (North)	0.06	0.63	0.33	0.52	0.10	0.13
15°	0.13	0.79	0.47	0.55	0.18	0.17
30°	0.26	0.98	0.66	0.60	0.34	0.28
45°	0.47	0.84	0.87	0.66	0.60	0.43
60°	0.76	0.70	0.95	0.73	0.95	0.40
75°	0.92	0.61	0.79	0.84	0.68	0.73
90° (East)	0.60	0.54	0.67	0.97	0.40	0.88
105°	0.34	0.50	0.56	0.85	0.22	0.95
120°	0.17	0.48	0.46	0.67	0.13	0.77
135°	0.08	0.47	0.37	0.55	0.08	0.57
150°	0.05 (+)	0.48	0.31	0.51	0.06	0.36
165°	0.04 (+)	0.53	0.28	0.50	0.07	0.19
180° (South)	0.06	0.63	0.33	0.52	0.10	0.13

Table A.7. Statistics for best fitting multivariate models and factors. Univariate and full models giving best fit by group. MJ 180º = May-June 180º wind component, MJ 175º = May-June 175º wind component, MJ 90º = May-June 90º wind component, FHS = flathead sole total biomass at given lag post settlement. AOw = winter Arctic Oscillation index and PDOs = summer Pacific Decadal Oscillation anomaly. Superscript denotes polynomial term, while sign within parentheses identifies nature of statistically significant relationship and accompanying number is the term p-value.

		EBS group			
	Factor 1	Factor 2	Factor 3	Factor 4	AICc value
Univariate Model	Lag 2 FHS^2 (-, 0.009)				66.33
Full model	MJ 180° (+, 0.013)	Lag 2 FHS^2 (-, <0.001)	AOw (-, 0.046)	PDOs (-, 0.007)	60.67
		Eastern group			
	Factor 1	Factor 2	Factor 3	Factor 4	AICc value
Univariate Model	AOw (-, 0.008)				81.79
Full model	MJ 90° (-, 0.004)	Lag 2 FHS^2 (-, 0.014)	AOw (-, <0.001)		72.96
		Western group			
	Factor 1	Factor 2	Factor 3	Factor 4	AICc value
Univariate Model	Lag 2 FHS^2 (-, 0.006)				59.57
Full model	MJ 175° (+, 0.004)	Lag 1 FHS^2 (-, <0.001)	PDOs (-, 0.003)		55.23

Appendix B:

Auxiliary Connectivity Analyses

Introduction

Assumptions of our connectivity study have the potential to significantly influence our results. Here, we explore the implications of two assumptions on retention and connectivity: (1) 60-d larval period, ignoring any potential additional advection during the megalops stage, and (2) the choice of our connectivity grid. Regarding the former, in a sensitivity analysis we examined the effects of an extended 90-d larval period on connectivity patterns to consider the possibility that megalopae continue to be advected similarly to crab zoeae. Regarding the latter, we conducted additional connectivity analyses using an alternative grid based on ecoregions as defined by the Bering Ecosystem STudy-Bering Sea Integrated Ecosystem Research Program (BEST-BSIERP, see http://bsierp.nprb.org/). This allowed us to test the sensitivity of our results to an alternative connectivity region geometry, which has larger grid size than the one we selected.

Methods

For the extended larval period analyses, a larval period of 90-d was assumed *in lieu* of the 60-d period employed in the analyses reported in Chapter 2. For the alternate grid-based analyses, the ArcGIS shapefile used as the basis of this grid was obtained from an online data repository at http://bsierp.nprb.org/. All other methods are as described in Chapter 2. For simplicity we only examined connectivity at the bulk level for both sensitivity analyses, with all depths being considered together.

Results

Extended Larval Advection Period

Results for the extended larval period analyses were broadly similar to those reported in Chapter 2. As with the 60-d advection period, regions 1, 7 and 13 were important endpoint regions, with region 1 losing prominence in the 1990s while regions 7 and 13 became more prominent, while region 15 was a significant endpoint region during the early 1980s (Figs B.1a, 1b, 1d). Retention rates were generally slightly reduced relative to the 60-d results (Figs 2.8, 2.9, 2.10), but still high, with retained endpoints contributing greatly to the total number of endpoints in most major regions (Figs B.2, B.3, B.4). The most pronounced difference observed was reduced retention rates in the regions of the outer domain (12, 13, 14, 15) during the 1980s, with retention in all regions increasing during the 1990s (see Figs B.2, B.3, B.4, B.5 versus Figs 2.8, 2.9, 2.10). Reduced retention during the 1980s was offset by weak offshore transport into the Bering Sea basin and regions of the continental slope (Fig. B.5), trends which weakened during the 1990s (Fig. B.5). Weak persistent onshore advection to the north/northwest and originating in the outer domain was observed beginning in the early 1990s. Strongest connectivity continued to be along-domain, with the strongest cross-domain connectivity being onshore and observed between the southern portions of the middle and outer domains (Fig. B.5).

BEST-BSIERP Alternative Connectivity Analyses

For analyses using the alternative connectivity grid, retention rates were high for all major source regions (Fig. B.6), comparing well to results for the custom grid (Fig. 2.11). Strongest exchange between the middle and outer domains was onshore in direction and limited

to the southern regions of both domains (regions 3 and 4, Fig. B.6). Within the middle domain, highly variable transport rates were observed between the southern middle domain (region 3) and the northern middle domain (region 6), (Fig. B.6), as compared to more sustained transport northwards with the custom grid (Fig. 2.11). Transport between regions of the outer domain was limited and in a northwesterly direction (Fig. B.6), versus stronger connections in the same direction using the custom grid, which employs more constrained regions in this area. In general agreement with the custom grid, the Pribilof Islands area (region 5) received limited numbers of floats from adjoining regions of both the middle and outer domain while exporting floats primarily to the northern middle domain, though a variable connection was observed with the southern middle domain during the 1980s (Fig. B.6, Fig. 2.11). Finally, the regions of the inner domain (regions 2 and 7) were not significant recipients of floats from any other release region (Fig. B.6).

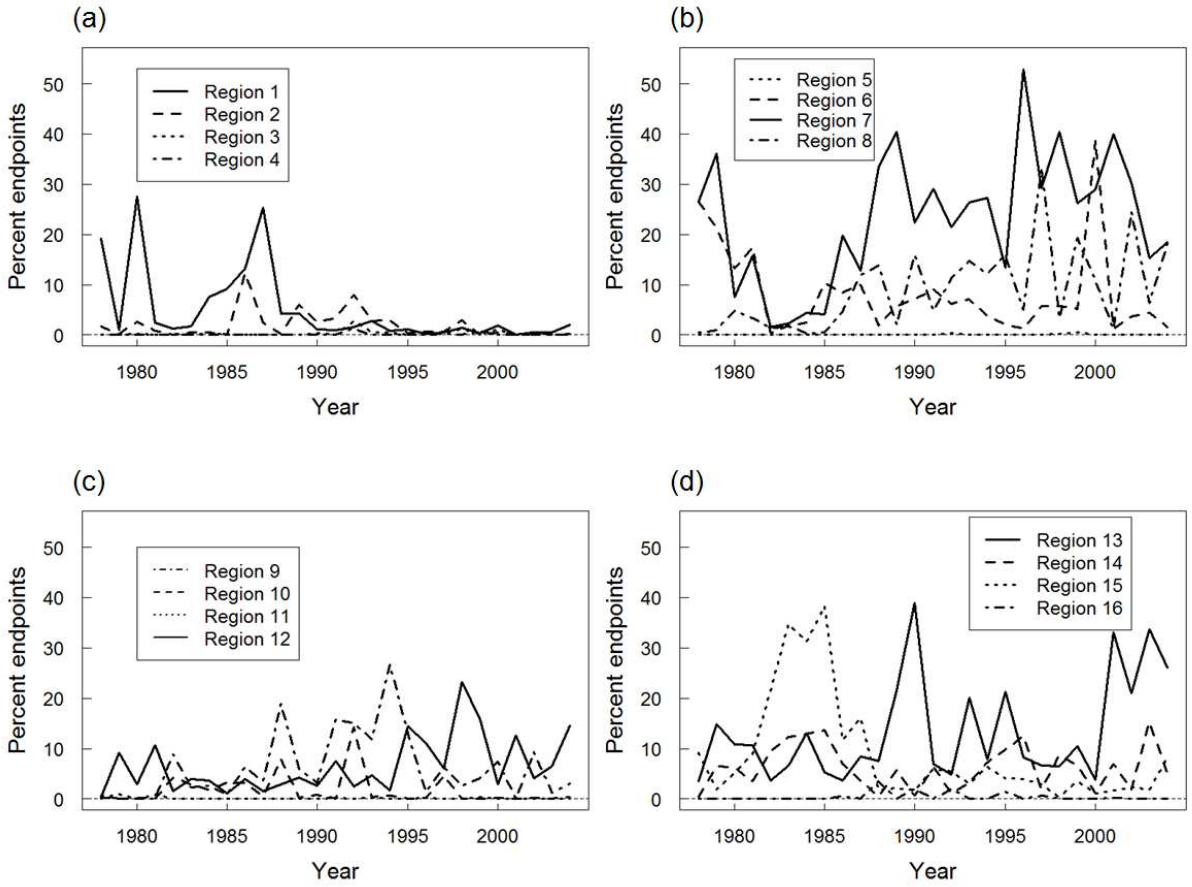

Figure B.1. Extended advection period float endpoint trends. Trends in percentages of float endpoints in (a) regions 1-4, (b) regions 5-8, (c) regions 9-12 and (d) regions 13-16. for 90-d extended advection period. Note trends for region 7 comprising the southern middle domain and region 13, the Pribilof Islands region. Also, note high endpoint rates in region 15 during early 1980s. For comparison to the results under the 60-d advection period, see Fig. 2.6.

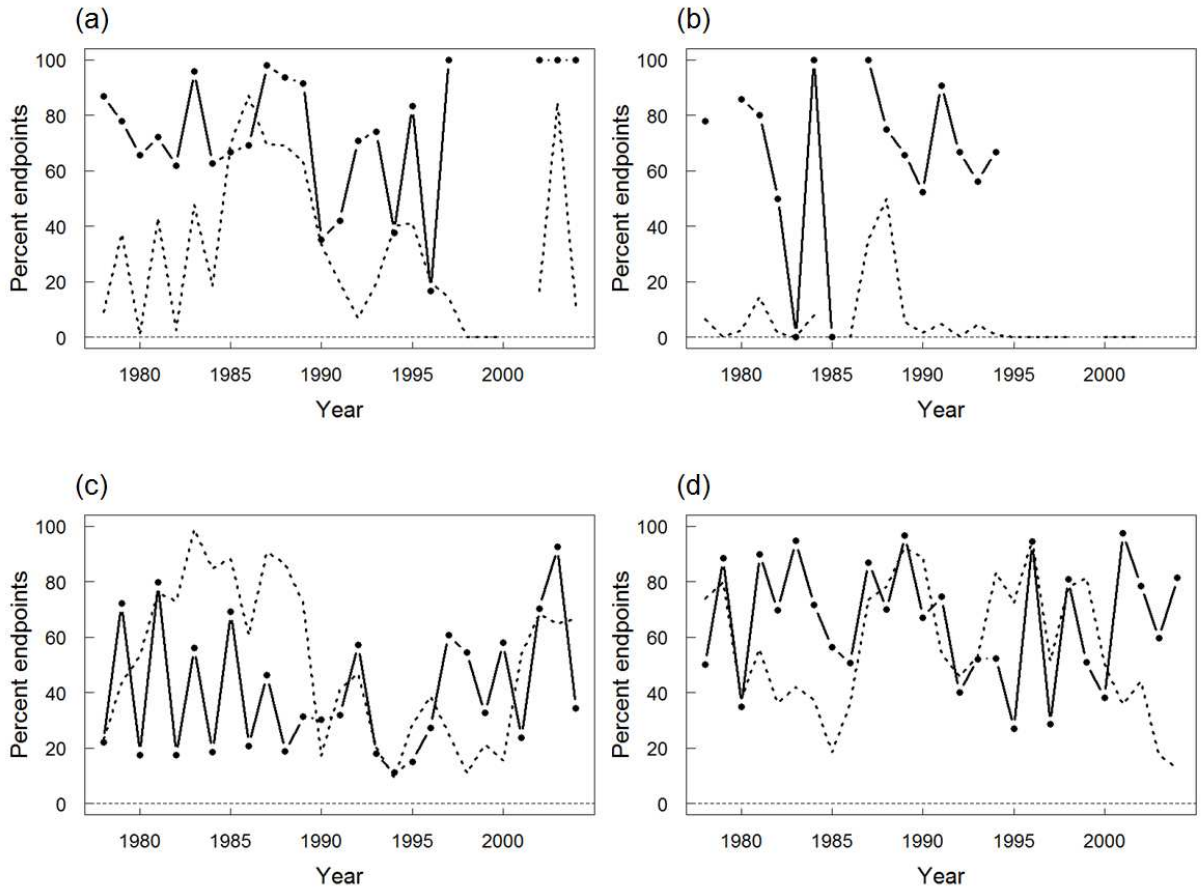

Figure B.2. Retention dynamics for regions 1, 2, 6 and 7. Trends in percentage of retained floats (solid line with points) and percentage of total number endpoints within region accounted for by retained floats (dashed line) for regions (a) 1 (b) 2 (c) 6 and (d) 7 for the extended 90-d advection period. Breaks in lines indicate years in which no floats originated in a given region. For comparison to the results under the 60-d advection period, see Fig. 2.8.

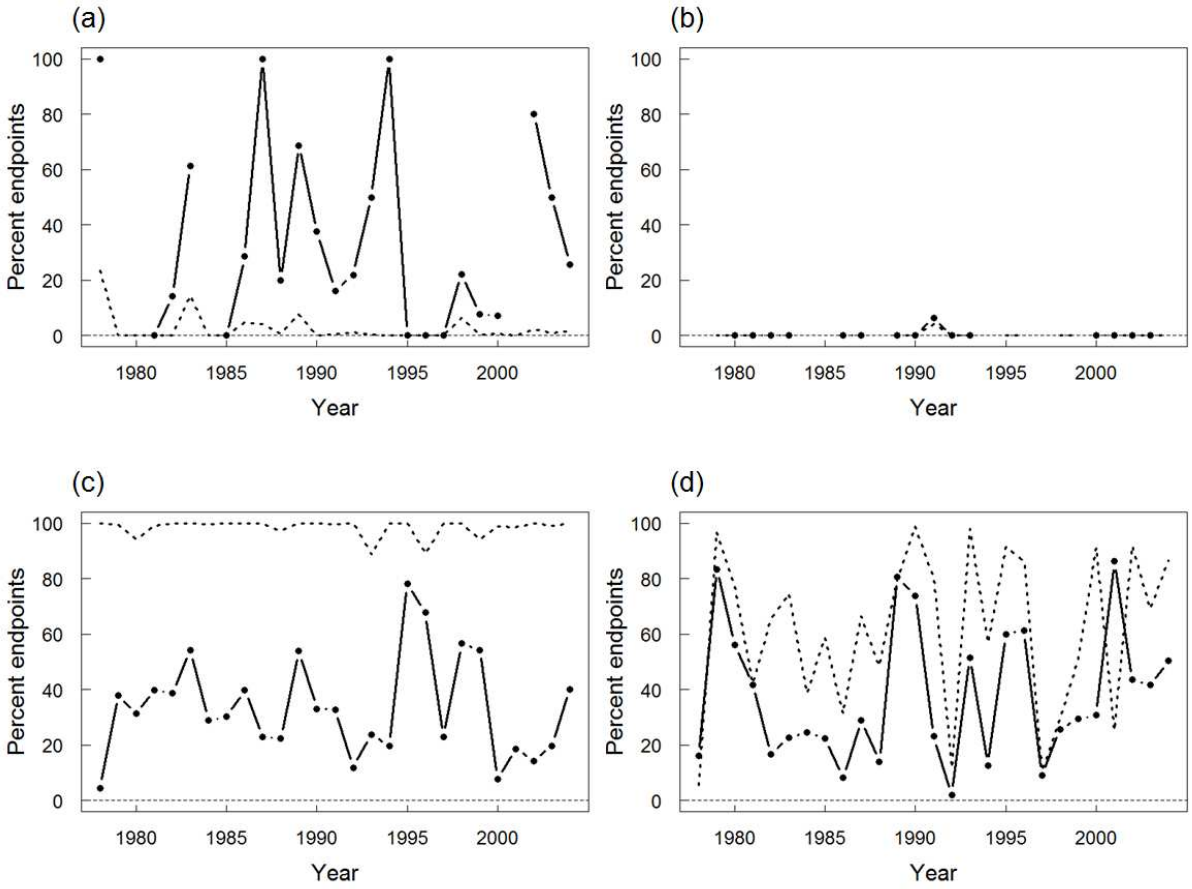

Figure B.3. Retention dynamics for regions 8, 11, 12 and 13. Trends in percentage of retained floats (solid line with points) and percentage of total number endpoints within region accounted for by retained floats (dashed line) for regions (a) 8 (b) 11 (c) 12 and (d) 13 for the extended 90-d advection period. Breaks in lines indicate years in which no floats originated in a given region. For comparison to the results under the 60-d advection period, see Fig. 2.9.

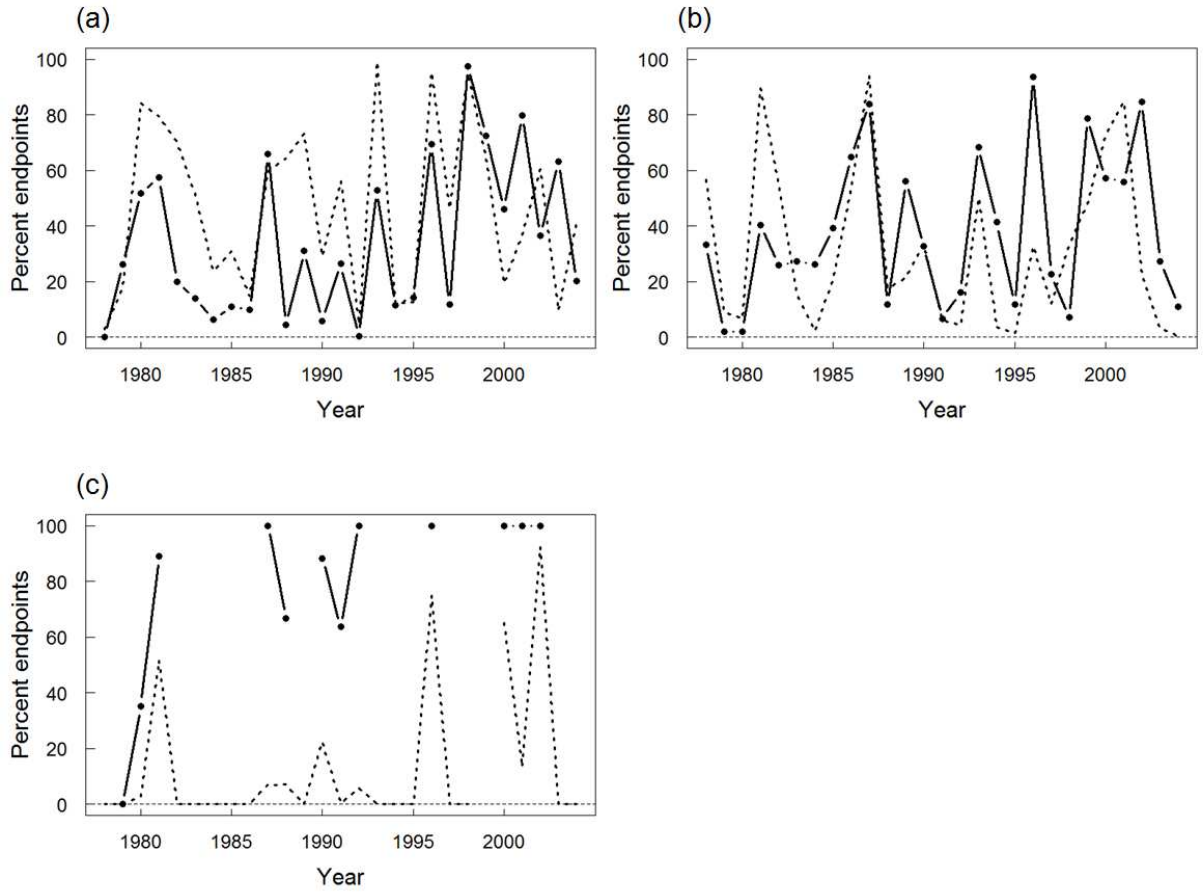

Figure B.4. Retention dynamics for regions 14, 15, and 18. Trends in percentage of retained floats (solid line with points) and percentage of total number endpoints within region accounted for by retained floats (dashed line) for regions (a) 14 (b) 15 and (c) 18 for the extended 90-d advection period,. Breaks in lines indicate years in which no floats originated in a given region. For comparison to the results under the 60-d advection period, see Fig. 2.10.

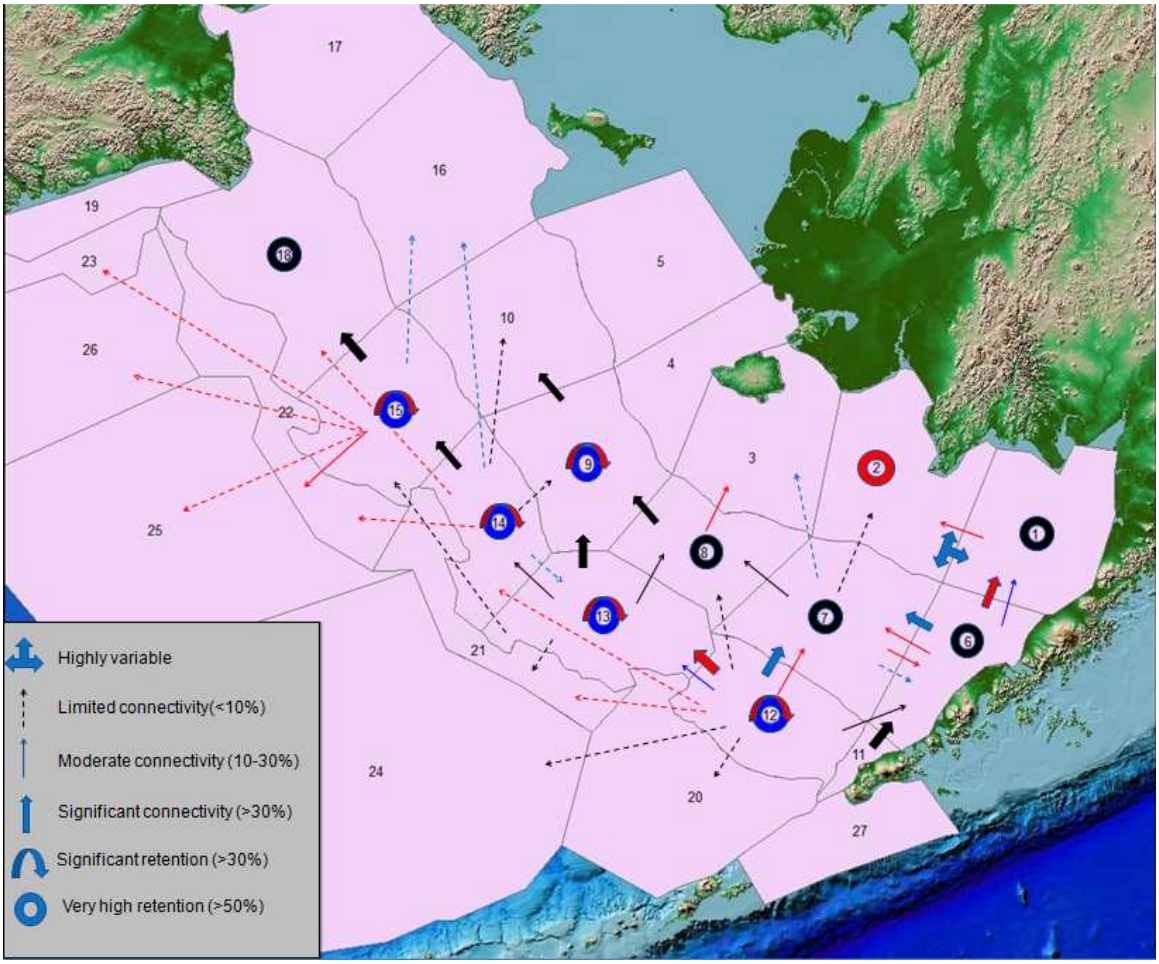

Figure B.5. Sustained extended period bulk connectivity and retention trends. Trends in bulk long-term retention and connectivity patterns under the extended 90-d larval period. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004. For comparison to the results under the 60-d advection period, see Fig. 2.11.

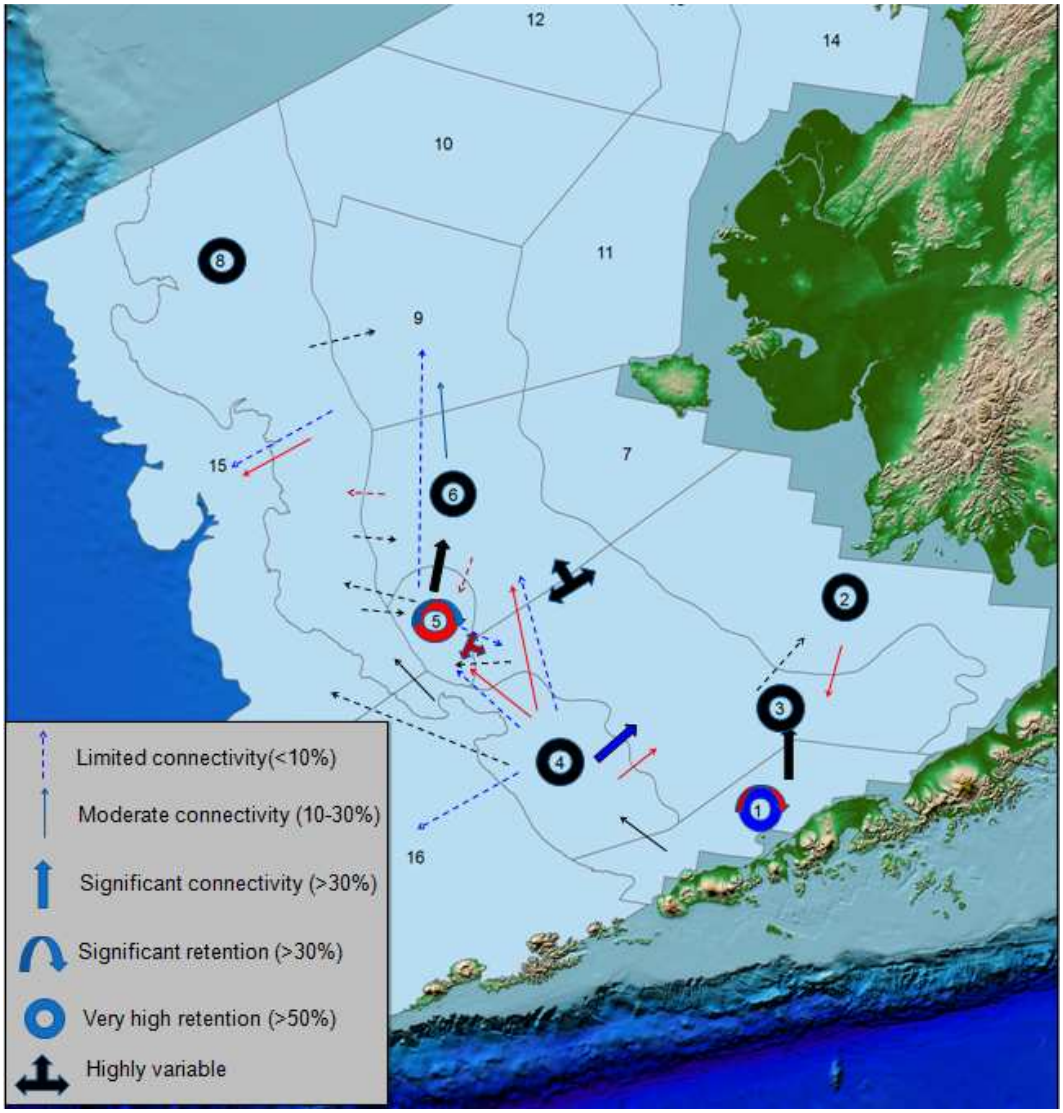

Figure B.6. Sustained bulk connectivity and retention trends. Trends in bulk long-term retention and connectivity patterns for the alternative BEST-BSIERP connectivity grid with 60-d advection period. Black denotes full time period, 1978-2004, red denotes 1978 to 1990, and blue denotes 1991-2004. For comparison to the results under the original grid, see Fig. 2.11.

Appendix C:

Alternative Analytical Approaches and Results

Introduction

Several alternative analytical approaches were evaluated for comparison against the threshold-correlation approach reported in Chapter 3. These analyses and their results were excluded from that chapter due to analytical limitations, in the interest of brevity, and due to generally disappointing results, associated particularly with high variability of the environmental factors and resultant uncertainty in the estimates based on those data. For these analyses, the following procedures were employed:

1. Exploratory correlation analyses (not adjusted for autocorrelation) comparing trends in environmental factor sample means at the model endpoints against trends in the same juvenile crab recruitment index used in the analyses reported in Chapters 1 and 3.

2. Simple linear and multiple regression analyses comparing means of the environmental factors at model endpoints against the same juvenile crab recruitment as above.

3. Distribution-based analyses combining qualitative visual interpretation of both probability density functions and empirical cumulative distribution functions (ECDFs) with quantitative analyses employing Kolmogorov-Smirnov tests, again focusing on conditions at the model endpoints. Crab recruitment to the 30-50 mm carapace width (CW) interval was classified into three recruitment bins, allowing comparison of conditions at the endpoints for years with low, moderate and high recruitment.

4. Geographically weighted regression (GWR) modeling, which allows relationships between crab recruitment trends and environmental factors to vary in space, with factors being

analyzed singly and in combination to allow for complimentary/interactive effects (Brunsdon et al. 1998).

As in Chapter 3, environmental factors investigated through these methodologies included (with lags in years post-settlement); near bottom temperature (NBT, 0, 1 and 2 yr), sea surface temperature (SST, 0 yr), surficial sediment class (0 yr), catch per unit effort (CPUE, in kg/Ha) for Pacific cod, and both yellowfin and flathead sole (1 and 2 yr) and densities (in crabs/km^2) of 30-50 mm CW juvenile Tanner crabs (0 and 1 yr) and 70-89 mm CW large juvenile male Tanner crabs (1 and 2 yr). Of note, SST was not investigated using Kolmogorov-Smirnov tests/ ECDFs due to issues with integrating model SST data encountered at the time those analyses were conducted.

Methods

Data

See the methods section in Chapter 3 for descriptions of data, hydrodynamic model specifications, and processing methodologies. Except where otherwise noted, primary analytical software was R version 2.14 (R Development Core Team 2005).

Regression Analyses

For regression analyses, sample means were calculated for each environmental factor as:

$$\overline{x_{ij}} = \frac{1}{N} \sum_{k=1}^{N} x_{jk}, \qquad \text{[eq. C-1]}$$

where $\bar{x}$ = the sample mean in year *i* for environmental factor *j*. These time series were then compared against standardized abundance residuals calculated from the 30-50 mm CW juvenile

crab index as in Chapter 3 (eq. 3.3), using simple linear and multiple regression modeling procedures. To simplify the model fitting process, factors were selected on the basis of the results reported in Chapter 3, and using results of stepwise model selection using linear modeling. Strongest factors were then manually incorporated into models for final analysis. To compensate for autocorrelation present in the juvenile crab residual series, in accordance with procedures employed in Chapter 1, generalized least squares (GLS) procedures incorporating first-order autocorrelation were employed in these final analyses (eq. 1.4). Due to poor initial results, we did not apply model selection criteria (i.e. small sample size Akaike Information Criterion (AICc)). Statistical significance of all model parameters was assessed at $\alpha = 0.05$.

Correlation Analyses

For correlation analyses, time series of the environmental factors as calculated above were compared against our 30-50 mm CW juvenile crab index using basic correlation procedures. Methods to account for autocorrelation were not employed in these analyses, due to both their exploratory nature and weak initial results, which did not support further analysis. Statistical significance of correlations was calculated as in Chapter 3 (eq. 3.10).

Kolmogorov-Smirnov Tests

We adapted the methods of Perry & Smith (1994) to test for associations between variability in environmental conditions at model-estimated settling locations and juvenile Tanner crab recruitment patterns. Empirical cumulative distribution functions were calculated for the values of each environmental variable at modeled settling locations within each year:

$$f(t) = \frac{1}{n} \sum_{i=1}^{n} 1\{x_i \leq t\}, \qquad \text{[eq. C-2]}$$

where n = sample size, x_i is the observed value at site, t is a given threshold value and *1* is the indicator value summed over all sites meeting the criteria.

To maintain a number of comparisons that would be both reasonable and manageable, ECDFs were then calculated for each factor for three representative release years corresponding to low recruitment (1982, 1990 and 1991), moderate recruitment (1981, 1988 and 1997) or high recruitment (1986, 1998 and 2001) to our juvenile crab index. These were then plotted for visual comparison against a second reference distribution for the given factor and chosen from one of the years listed. This reference distribution was chosen from a recruitment category based on whether a between- or within-recruitment category comparison was desired. Empirical cumulative distribution functions were assigned a score for being lower (signifying prevalence of the factor at lower values relative to the reference distribution), higher (signifying prevalence at higher values relative to the reference distribution) or ambiguous (no clearly discernible trend relative to the reference distribution). Scores were tallied as a percentage of the total number of comparisons for each category pairing to determine whether an effect might be present.

As a statistical test for similarity between the data distributions, two-sample Kolmogorov-Smirnov test statistics were calculated for each pairing of data distributions. The Kolmogorov-Smirnov statistic (eq. 3) tests for similarity between two data distributions by determining the point of maximum vertical difference (D) between two data distributions (Perry & Smith, 1994):

$$D_n = sup_x|F_n(x) - F(x)|, \qquad \text{[eq. C-3]}$$

where sup_x = the supremum of the set of distances between the distributions and $F_n(x)$ and $F(x)$ are the distributions being compared.

To determine significance, the value of D_n is then compared to the critical value, D_α:

$$D\alpha = c(\propto)\sqrt{\frac{n_1+n_2}{n_1 n_2}}, \qquad \text{[eq. C-4]}$$

where $c(\alpha)$ = a coefficient determined by the desired α of the test, and n_1 and n_2 are the sample sizes of the distributions being compared (Wessel 2013). Statistical significance was assessed at $\alpha = 0.05$.

Geographically Weighted Regression Modeling

The ArcGIS 10.1 Spatial Statistics Geographically Weighted Regression toolset was used to conduct GWR analyses (ESRI 2011). The cross-validation (CV) bandwidth selection option was employed with default settings. Initial factor selection was based on performance of factors in the Chapter 3 analyses and in the other analytical procedures discussed here. Both single-factor and multi-factor models were attempted.

Results

Results from these analyses do not generally offer strong support for the relationships hypothesized among the factors, nor do they provide good support for the findings reported in Chapter 3.

Correlation Analyses

Correlation analyses suggest that only near bottom temperature lagged 2 yr after settling and densities of 30-50 mm CW crab lagged for effect 1 yr after settling were statistically related to crab recruitment ($r > 0.4$, Table C-1), with both correlations being positive. However,

while a positive correlation between near bottom temperature and crab recruitment is biologically reasonable, a positive relationship between juvenile crab densities and crab recruitment is inconsistent with the hypothesized cannibalistic relationship. Rather, this relationship likely arises due to autocorrelation in crab recruitment trends that is reflected in both the abundance index and in crab densities.

Regression Analyses

Regression analyses were generally disappointing, with only a few significant relationships being indicated (Table C-2). Surprisingly, the only multi-term model in which all terms were significant combined yellowfin sole lagged 2 yr after settlement and sediment class, neither of which shows much relation to crab recruitment trends when considered on its own. However, inconsistent with a predatory effect, yellowfin sole is suggested to have a positive relationship with crab recruitment, suggesting a factor external to the model system may be influencing both stocks. A positive relationship with crab recruitment is also observed for surficial sediment class, with this being consistent with the hypothesis that fine grain sediments provide sanctuary for early juvenile Tanner crabs. For single factor models, the only identified significant factor was Pacific cod CPUE, lagged 2 yr after settlement, which had a negative relationship to crab recruitment, consistent with a predatory effect (Table C-1).

CDFs and Kolmogorov-Smirnov Tests

For each of the three recruitment categories examined, ECDFs demonstrated significant variability in all comparisons between year classes selected from the same recruitment category, although adjacent years tended to be more similar than those more temporally distant from each other (Figs C-1, C-2). This pattern of dissimilarity was repeated in the comparisons

between recruitment categories. The only exceptions to this pattern were observations of surficial sediment class at the endpoint locations, with these being notably similar in multiple comparisons, both within and between recruitment categories. These findings were supported by the results of the two-sample Kolmogorov-Smirnov tests, which suggested that all distributions were significantly different from each other, including those that appeared to be visually very similar (Fig. C-3, Table C-3). The limited subset of years used for each recruitment period (3), and consequently limited number of years overall (9) for which analyses were conducted, however, comprises a potentially serious limitation in the ECDF based analyses.

Weak vs. Weak Recruitment

Comparisons within the low recruitment category, in which environmental conditions for the 1982, 1990 and 1991 year classes were compared, yielded some interesting results. This selection of years was able to capture apparent differences in conditions before (1982) and after (1990 and 1991) the proposed 1989 regime shift (Hare & Mantua 2000), while also highlighting short-term interannual changes in conditions. Relative to the post-regime year classes, the 1982 year class was exposed to lower densities of both flathead and yellowfin sole, but higher densities of Pacific cod. In addition, the 1982 year class experienced generally warmer near bottom temperatures, and reduced densities of both categories of juvenile crab. The 1990 and 1991 year classes experienced conditions that, while broadly similar in comparison to those experienced by the 1982 year class, were still statistically different. While long-term trends may exist, differential exposure, likely as a result of a combination of both short-term variability in the environment itself and interannually variable larval advection

paths, is still a major component. Results for moderate vs. moderate and high vs. high comparisons, which we do not report in detail here, were generally similar with high variability observed between years, and no clear trends.

Weak vs. Moderate Recruitment

Comparisons of recruitment factor ECDFs between weak and moderate recruitment year classes were generally inconclusive (Table C-4). The ECDFs for 1982 demonstrated markedly different relationships to those of the moderate recruitment years than did those for 1990 or 1991, often showing opposing trends (i.e. Fig. C-1). Empirical cumulative distribution functions for these later years demonstrated similar relationships to those of the moderate recruitment years. Of the environmental factors investigated, settling year NBT, yellowfin sole 1 yr after settling, flathead sole 2 yr after settling and 70-89 mm CW male crab 1 and 2 yr after settling demonstrated possible trends relative to crab recruitment. Low recruitment years were associated with warmer settling year NBT temperatures, higher densities of 70-89 mm CW crab and flathead sole, and lower densities of yellowfin sole than were moderate recruitment years in 6 of 9 comparisons (Table C-4).

Weak vs. High Recruitment

Comparisons of recruitment factor ECDFs between weak and high recruitment year classes were generally highly variable, lacking clear trends in most factors. The notable exception to this was 70-89 mm CW subadult male crab density in the year after settling. In this case, weak year classes were associated with higher densities of crab in 8 of 9 comparisons, relative to high recruitment year classes (Table C-5). Results for Pacific cod, yellowfin sole and NBT were also suggestive (Table C-5). For both yellowfin sole and Pacific cod, relative to high

recruitment year classes, low recruitment was associated with higher CPUE values at estimated settling locations 1 yr after settling in 5 of 9 comparisons (Table C-5). Finally, in 6 of 9 comparisons lower endpoint NBT at lags of 0 (settling year) and 1 year after settling were associated with low recruitment year classes relative to those associated with high recruitment year classes.

Moderate vs. High Recruitment

As in the comparisons of ECDFs for weak recruitment years against moderate recruitment years, comparison of moderate vs. high recruitment years gave ambiguous results (Table C-6). A possible trend was observed for Pacific cod lagged for a predatory effect 2 yr after settling, with moderate recruitment years being associated with higher densities of cod at the model end points in 6 of 9 comparisons. In addition, NBT at the endpoint was lower for the moderate recruitment year in 7 of 9 comparisons when lagged for effect 2 yr after settling, and in 6 of 9 comparisons when lagged for effect 1 yr after settling. Finally, flathead sole CPUE lagged 2 yr after settling was lower at the endpoints for the moderate recruitment year classes in 6 of 9 comparisons (Table C-6).

Geographically Weighted Regression Modeling

Attempts to conduct GWR analyses were, as a whole, unsuccessful. Multifactor models experienced severe issues with multicollinearity, which prevented successful fitting. Initial attempts to fit a model surface for a single factor were more successful, but due to the great number of endpoint locations for which individual models were to be calculated (>10,000), required significant computational resources and time to successfully fit a given model surface. In light of the limited use that was to be made of the results, the number of years for which

models were to be calculated and the number of factors to be investigated, it was decided that further examination using this procedure was not warranted at this time.

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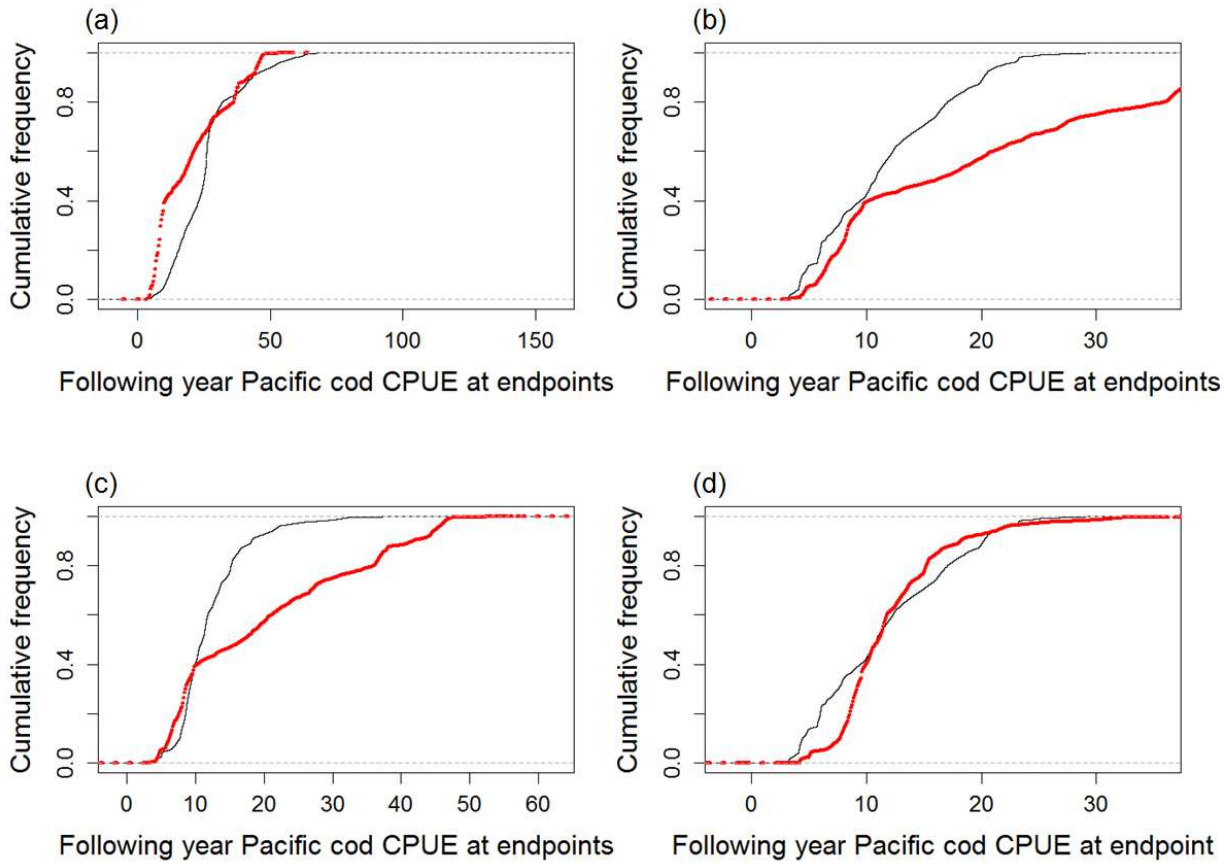

Figure C-1. Comparison of trends in Pacific cod CPUE (I). Comparison of cumulative distribution functions for Pacific cod CPUE at 60 day endpoints for: (a) 1982 (black, low recruitment) vs. 1981 (thick red line, medium recruitment), (b) 1990 (black, low recruitment) vs. 1981 (thick red line, medium recruitment), (c) 1991 (black, low recruitment) vs. 1981 (thick red line, medium recruitment) and (d) 1990 (black, low recruitment) vs. 1991 (thick red line, low recruitment). Of note is the greater similarity between adjacent years than between years with similar recruitment levels.

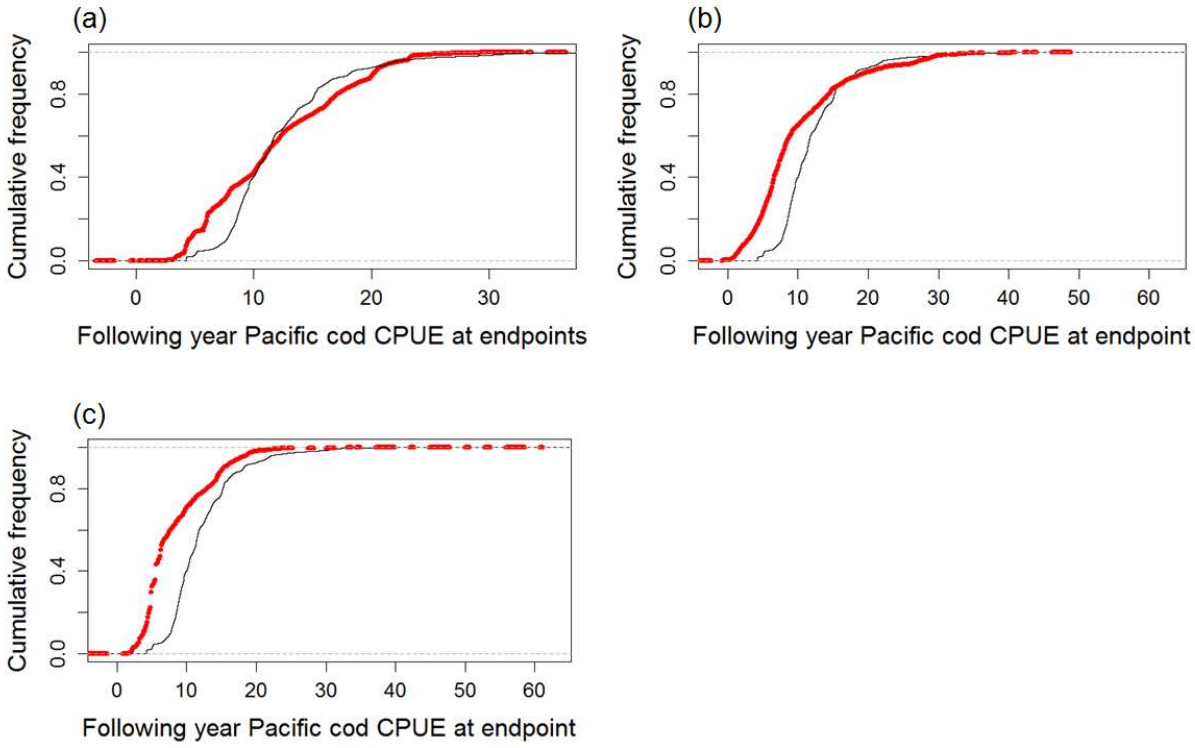

Figure C-2. Comparison of trends in Pacific cod CPUE (II). Comparison of cumulative distribution functions for Pacific cod CPUE at 60 day settling points for a representative low recruitment year class (1991, black lines) versus (thick, red lines): (a) low recruitment year class (1990), (b) moderate recruitment year class (1997), and (c) a high recruitment year class (2001). All variables investigated showed similar inter- and intra-recruitment class differences.

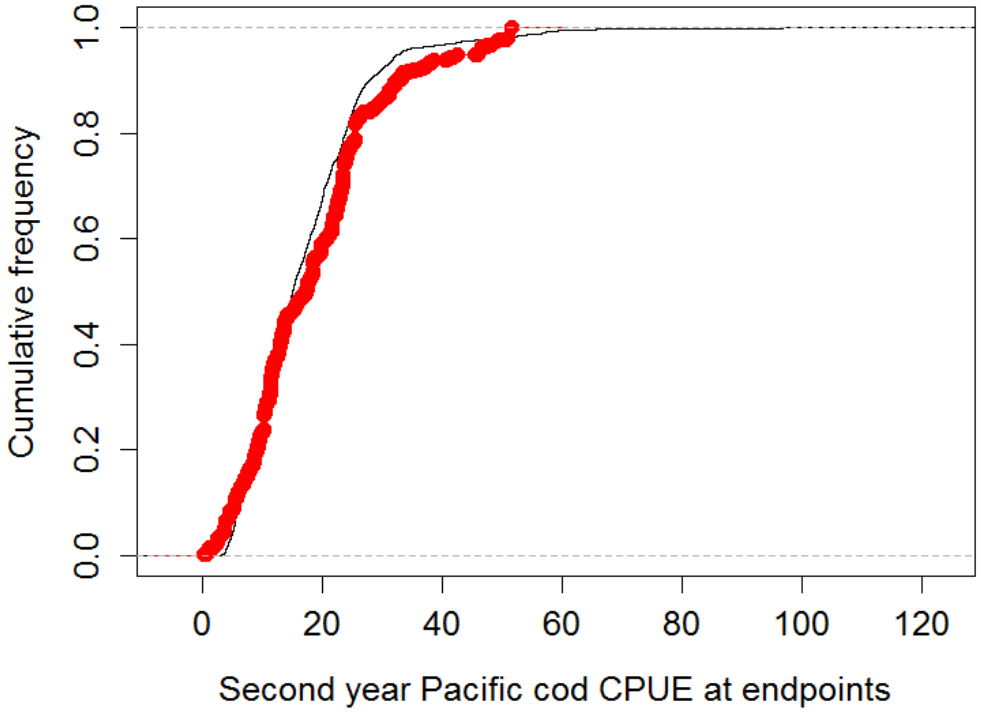

Figure C-3. Comparison of Pacific cod CPUE trends. Comparison of cumulative distribution functions for Pacific cod CPUE for two moderate recruitment years: 1981 (black) and 1997 (red).

Table C-1. Correlations and *r*-squared values for environmental factors. Values of correlations between 30-50 mm carapace width juvenile crab recruitment index and environmental factors, with attendant *r*-squared values.

Factor	sign	*r*-squared
Pacific cod, lag 1	-	0.02028
Pacific cod, lag 2	-	0.08726
Yellowfin sole, lag 1	+	0.00259
Yellowfin sole, lag 2	+	0.0064
Flathead sole, lag 1	-	0.01545
Flathead sole, lag 2	+	0.00092
Retention	+	0.09709
Sediment class	+	5.3E-05
Sea surface temperature	+	0.0183
Near bottom temperature, lag 0	+	0.07712
Near bottom temperature, lag 1	+	0.06922
Near bottom temperature, lag 2	+	0.19634
30-50 mm CW juvenile crab, lag 0	+	0.10266
30-50 mm CW juvenile crab, lag 1	+	0.16314
70-89 mm CW male crab, lag 1	-	0.04448
70-89 mm CW male crab, lag 2	+	0.01302

Table C-2. Example regression model output. Representative example regression model with results. Factors are: NBT, near bottom temperature; Pcod, Pacific cod; Yfin, yellowfin sole; FHS, flathead sole; Sed, sediment class. Units for Pacific cod, yellowfin sole and flathead sole, kg/Ha and for NBT, °C. The numerals 0, 1 and 2 denote lags of 0, 1 and 2 yr post release.

Model	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
1	Pcod1 (-1.24e-2, 0.65)					
2	Pcod2 (-4.46e-2, 0.04)					
3	Pcod1 (-6.21e-3, 0.80)	Pcod2 (-4.40e-2, 0.05)				
4	Pcod1 (8.76e-2, 0.25)	Pcod2 (-5.17e-2e, 0.49)	Pcod1:Pcod2 (4.41e-3, 0.19)			
5	Pcod1 (-6.25e-2, 0.86)	Sed (-1.46e-1, 0.90)	Pcod1:Sed (6.88e-3, 0.89)			
6	Pcod2 (2.71e-1, 0.42)	Sed (9.1e-1, 0.32)	Pcod2:Sed (-4.46e-2, 0.34)			
7	Yfin1 (2.36e-1, 0.17)	Sed (1.7844, 0.15)	Yfin1:Sed (-0.0329, 0.18)			
8	Yfin2 (2.77e-1, 0.03)	Sed (2.0994, 0.04)	Yfin2:Sed (-0.0376, 0.04)			
9	Yfin1 (2.14e-1, 0.37)	Yfin2 (2.21e-1, 0.25)	Sed (3.1261, 0.07)	Yfin1:Yfin2 (-7.4e-5,0.79)	Yfin1:Sed (-3.04e-2, 0.36)	Yfin2:Sed (-2.9e-2, 0.28)
10	Pcod1 (-1.48e-2, 0.60)	FHS1 (-7.83e-2, 0.15)	NBT0 (2.68e-1, 0.18)			
11	Pcod1 (9.74e-2, 0.40)	FHS1 (5.78e-2, 0.71)	NBT0 (1.75, 0.06)	Pcod1:NBT0 (-4.44e-2, 0.22)	FHS1:NBT0 (-4.79e-2, 0.20)	Pcod1:FHS1 (2.02e-4, 0.97)
12	NBT0 (1.94e-3, 0.99)	NBT1 (-4.17e-2, 0.87)	NBT2 (1.75e-1, 0.48)			
13	NBT0 (6.32e-1, 0.38)	NBT1 (1.54, 0.37)	NBT2 (4.86e-1, 0.63)	NBT0:NBT1 (-4.43e-1, 0.21)	NBT0:NBT2 (1.85e-1, 0.48)	NBT1:NBT2 (-2.16e-1, 0.69)
14	NBT0 (5.56e-2, 0.75)	NBT1 (-1.35e-1, 0.58)				
15	NBT0 (4.36e-1, 0.48)	NBT1 (2.15e-1, 0.72)	NBT0:NBT1 (-1.58e-1, 0.51)			

Table C-3. Example Kolmogorov-Smirnov statistics. Kolmogorov-Smirnov *D* test statistic values and p-values for 1991 (a moderate recruitment strength year) vs. 2001 (a high recruitment strength year). All other comparisons had similarly significant results.

Factor	*D*	p-value
Pacific cod, following year (year 1)	0.5062	<0.0001
Yellowfin sole, following year (year 1)	0.4238	<0.0001
Flathead sole, following year (year 1)	0.3092	<0.0001
Pacific cod, second year (year 2)	0.3522	<0.0001
Yellowfin sole, second year (year 2)	0.4823	<0.0001
Flathead sole, second year (year 2)	0.2630	<0.0001
Sediment class, settling year (year 0)	0.1894	<0.0001
NBT, settling year (year 0)	0.6798	<0.0001
NBT, following year (year 1)	0.8250	<0.0001
NBT, second year (year 2)	0.8189	<0.0001
Juvenile density, settling year (year 0)	0.6982	<0.0001
Juvenile density, following year (year 1)	0.8090	<0.0001
Large male density, following year (year 1)	0.4088	<0.0001
Large male density, second year (year 2)	0.4214	<0.0001

Table C-4. Comparisons of cumulative distribution functions (I). Comparisons of cumulative distribution functions for low recruitment vs. moderate recruitment year classes. LRY = low recruitment year class. Factors are: Juv, 30-50 mm carapace width (CW) Tanner crab; Lrg_crab, 70-89 mm CW male crab; NBT,; near bottom temperature; PCod, Pacific cod; Yfin, yellowfin sole; FHS, flathead sole; Sediment, sediment class; Retention; Retention within study area. Units for 30-50 mm and 70-89 mm CW crab are crab/km^2, for NBT, °C and for Pacific cod, yellowfin sole and flathead sole, kg/Ha. The numerals 0, 1 and 2 denote lags of 0, 1 and 2 yr post release. Higher/lower denotes whether low recruitment year class was associated with higher/lower values of the stated factor than those experienced by the moderate recruitment year class.

Factor	Number of comparisons LRY higher	Number of comparisons LRY lower	Number of ambiguous comparisons
Pcod1	4	4	1
Pcod2	4	5	0
Yfin1	1	6	2
Yfin2	3	4	2
FHS1	5	1	3
FHS2	6	3	0
NBT0	6	3	0
NBT1	2	4	3
NBT2	5	2	2
Juv0	3	4	5
Juv1	1	3	1
Lrg_crab1	6	2	1
Lrg_crab2	6	1	2
Sediment	3	4	2

Table C-5. Comparisons of cumulative distribution functions (II). Comparisons of cumulative distribution functions for low recruitment vs. high recruitment year classes. LRY = low recruitment year class. Factors are: Juv, 30-50 mm carapace width (CW) Tanner crab; Lrg_crab, 70-89 mm CW male crab; NBT,; near bottom temperature; PCod, Pacific cod; Yfin, yellowfin sole; FHS, flathead sole; Sediment, sediment class; Retention; Retention within study area. Units for 30-50 mm and 70-89 mm CW crab are crab/km^2, for NBT, °C and for Pacific cod, yellowfin sole and flathead sole, kg/Ha. The numerals 0, 1 and 2 denote lags of 0, 1 and 2 yr post release. Higher (lower) denotes whether the low recruitment year class was associated with higher (lower) values of the stated factor than those experienced by the high recruitment year class.

Factor	Number of comparisons LRY higher	Number of comparisons LRY lower	Number of comparisons ambiguous
Pcod1	5	4	0
Pcod2	5	2	2
Yfin1	5	3	1
Yfin2	5	3	1
FHS1	5	3	1
FHS2	4	5	0
NBT0	3	6	0
NBT1	2	6	1
NBT2	4	5	0
Juv0	2	5	2
Juv1	0	7	2
Lrg_crab 1	8	1	0
Lrg_crab2	4	4	1
Sediment	1	7	1

Table C-6. Comparisons of cumulative distribution functions (III). Comparisons of cumulative distribution functions for moderate recruitment vs. high recruitment year classes. MRY = moderate recruitment year class. Factors are: Juv, 30-50 mm carapace width (CW) Tanner crab; Lrg_crab, 70-89 mm CW male crab; NBT, near bottom temperature; PCod, Pacific cod; Yfin, yellowfin sole; FHS, flathead sole; Sediment, sediment class; Retention; Retention within study area. Units for 30-50 mm and 70-89 mm CW crab are crab/km^2, for NBT, °C and for Pacific cod, yellowfin sole and flathead sole, kg/Ha. The numerals 0, 1 and 2 denote lags of 0, 1 and 2 yr post release. Higher (lower) denotes whether moderate recruitment year class was associated with higher (lower) values of the stated factor than those experienced by the high recruitment year class.

Factor	Number of comparisons MRY higher	Number of comparisons MRY lower	Number of comparisons ambiguous
Pcod1	4	3	2
Pcod2	6	3	0
Yfin1	5	3	1
Yfin2	5	3	1
FHS1	3	5	1
FHS2	0	6	3
NBT0	3	5	1
NBT1	3	6	0
NBT2	2	7	0
Juv0	4	5	0
Juv1	2	6	1
Lrg_crab1	4	3	2
Lrg_crab2	1	4	4
Sediment	1	5	3